Snow Buntings *Plectrophenax nivalis*: the Behavioural Ecology and Site Use of an Itinerant Flock Species in the Non-breeding Season

Richard D. Smith

This thesis is submitted in candidature for the Degree of Doctor of Philosophy, Department of Zoology, University of Glasgow.

November 1994.

ACKNOWLEDGEMENTS

I am totally indebted to my supervisor Neil Metcalfe whose good nature must have been sorely tested in the past five years by the demands of a part-time absentee student. Not only was Neil brave enough (some might use a different adjective) to take me on, he was also primarily responsible for securing much of my funding. Neil's contribution to the direction and analysis of my work has been immense, and he has promptly and uncomplainingly passed extensive comments on the contents of this thesis and several other long and tedious manuscripts. I must also guiltily thank him for being my general dog's-body at Glasgow: printing, copying, procuring, administering, fabricating, liasing, etc., etc. way beyond the call of duty. Many thanks, Neil.

Two other persons deserve special mention for making this thesis happen. Des Thompson had a pivotal role in obtaining funding for the initial work on wintering Snow Buntings and parallel studies on the species' breeding biology. He then gave me the confidence to focus future work towards obtaining a higher degree. Des has also given me access to many Scottish Natural Heritage staff and facilities, and provided many stimulating ideas and criticisms. I am also indebted to Mick Marquiss for generating me with enthusiasm, providing practical and statistical advice and discussion, and commenting extensively and intelligently on an earlier draft of this thesis.

The study received funding from (in order of monetary value) the Natural Environment Research Council, Scottish Natural Heritage (formerly the Nature Conservancy Council, Scotland), Highlands and Islands Enterprise (formerly the Highlands and Islands Development Board), the Nuffield Foundation, the British Ecological Society, the Association for the Study of Animal Behaviour, Cairngorm Chairlift Company, Craignish Conservation Trust, the British Ornithologists' Union, and the British Trust for Ornithology. The Royal Society for the Protection of Birds provided accomodation during early 1988.

I am grateful for the help of a number of colleagues at Glasgow University, especially Martin Burns for computing advice. Liz Denton, Roddie MacDonald, Nozrat Mirzai and Caroline Askew all provided technical support. Thanks also to everyone at Rowardenan Field Station. Scottish Natural Heritage staff have been extremely cooperative, notably Allan Brown who introduced me to the magical world of computing. Marianne Robson, computing staff in Edinburgh and office staff at Achantoul, Aviemore have also been very helpful. The Meteorological Office at Achantoul gave access to weather records.

I also appreciate the contribution of Cairngorm Chairlift Company to this project. Tommy Paul, and latterly Tim Whittome, allowed me to work on the Ski Area, provided free chairlift tickets, and were generally responsive to my requests for help. Neil Baxter and the other rangers supplied daily weather records. The garage and road crews enabled me, and often my car, to get to my observation sites in some atrocious

weather conditions. Thanks also to the bus drivers for their tolerance, and everyone who mentioned seeing birds. Thanks are also due to Highlands and Islands Enterprise, the Royal Society for the Protection of Birds, the ski companies at Glen Shee and The Lecht, and the farmers and keepers at the Cabrach and Corgarff for letting me work on their land.

A number of friends and colleagues have given me assistance, advice, encouragement and floor space. I particularly wish to thank Adam Watson, Hector Galbraith, Phil Whitfield, Pat Monaghan, Keith Duncan, Dave Horsfield, Rab Rae, Colin and Margaret Daveson, Phil Atkinson, Steve Buckland, Dave Thompson, Chris Thomas, Stuart Mackay, Stuart Rae and Juan Carlos Senar. I also wish to thank all those who helped me trap birds, or contributed to my summer observations of Snow Buntings. Trapping data from other North-east Scottish sites were kindly provided by Rab Rae, Raymond Duncan, Mike Kimber, Ian Mackay, Mick Marquiss and Bob Procter. Colour-rings were copiously and promptly supplied by Mike Nicol and were very successful. Kevin Baker administered ringing activities at the B.T.O. I am also grateful to Alan and Tilly Smith for keeping their Reindeer from eating too much of the food that I provided for Snow Buntings, and Charlie Walpole, Ron Grant, George Macdonald Sr. and Jr., and Dai Davies for generally putting up with and helping me during the last few winters.

I must also thank the birds themselves for some great entertainment. Many, especially those which remained to breed in the Cairngorms, became unforgettable individuals. Hopefully, this thesis will go some way towards justifying their trapping and marking.

Finally, and by no means least, I would like to express my gratitude to the family and friends who have put up with and supported me through this 'writing-up' stage of the project. Phone calls and visits were more than welcome distractions, which kept me going in the dark months when everything was a chore and the tunnel seemed to have no end. Now, however, the real world beckons....

To my folks, Dorothy and David

DECLARATION

I declare that the work described in this thesis has been carried out by myself unless otherwise cited or acknowledged. It is entirely of my own composition and has not, in whole or in part, been submitted for any other degree.

RICHARD DAVID SMITH

November 1994

TABLE OF CONTENTS

SUMMARY

This thesis examines how extrinsic and intrinsic factors affect dispersal, foraging, aggression and energy reserves in a winter population of a small, migratory flocking bird, the Snow Bunting *Plectrophenax nivalis*. Previous observations of this species, and consideration of its northern ground-feeding open country niche, suggested that Snow Buntings were less likely to show as strong a degree of site fidelity as many other winter-studied species. This may therefore have led to opportunities for the Snow Bunting's winter behavioural ecology to diverge from that of more sedentary species.

The distribution of age and sex categories of wintering Snow Buntings was examined at eleven sites in North-east Scotland which varied markedly in altitude (and consequently habitat and climate). The proportions of adult males and adult females trapped at these sites increased with altitude, whilst the proportion of juvenile females decreased. Because males are the larger sex, and adult birds have the advantage of previous experience, the distribution of age and sex categories suggested that more elevated sites were of higher quality. Consequently, I suggest several environmental factors (reduced competition, fewer predators, and similarity to breeding conditions) which may be responsible for altitudinal segregation and argue that these may also help explain intraspecific latitudinal segregation patterns in this and other species.

More detailed observations of Snow Bunting numbers and behaviour were made at one high altitude site, Cairn Gorm, during 1987/88 to 1992/93. There was evidence that, even *within* this site, birds selected higher altitude feeding areas when possible. However, snowfalls caused some birds, particularly young or naive individuals or females, to leave the site, although population composition recovered during subsequent thaws.

The itinerant nature of the populations during winter was further evidenced by 44 movements of 20+km by individually-marked birds within winter (November-February) periods, and 134 other movements occurring over longer timespans. Several movements suggested that some birds may have selected higher altitude or higher latitude sites as they got older. A large proportion of birds visited Cairn Gorm only briefly: some 62% of the 74 individuals that had been marked elsewhere before arriving at Cairn Gorm were seen on only 1-3 occasions.

The factors affecting foraging efficiency were investigated by recording the behaviour of individuals at a feeding arena during 1551 time budgets. Both peck-rate whilst feeding and the amount of time spent feeding increased with flock-size and were greater early in a flock's feeding bout. After controlling for these variables, adults and/or birds with prior site experience achieved faster peck-rates than immatures and/or inexperienced Snow Buntings in both competitive and non-competitive situations; furthermore,

males had higher peck-rates than females, but only in large flocks. Residual peck-rate increased as naive individuals gained more site experience. Males, adults and experienced birds tended to spend more time feeding than their counterparts in early parts of feeding bouts although this effect was less obvious later in the feeding bout unless the flock size remained high. These differences were compounded by the tendency to find males, adults and/or experienced birds in favourable feeding environments (large flocks, central positions, early in the feeding bout), and with less need to manoeuvre for access to food.

Altogether, 12009 agonistic interactions were noted over five winters. Aggression was more frequent with increasing flock-size and in cold, snowy conditions. Winners were more likely to feed and/or to retain a feeding position soon after a fight than losers. As expected, males, the larger gender, won the majority (90%) of intersexual contests. However, contrary to most previous studies, within sex categories juveniles won the majority (60-70%) of contests with adults. This could not be attributed to differences in individual quality between contestants, but was associated with changes within individuals: rank dropped between an individual's first and second winters. There was no evidence that dominance status changed during the winter, or as resource value changed (as estimated by weather conditions or contest escalation). Also contrary to previous studies, birds with prior site experience won less contests than expected, although the differences were less marked (2-14%) than those observed between age groups.

Measurements of body-mass and visible fat deposits were used to estimate energy reserves of over 3000 trapped Snow Buntings (almost 1000 of these at Cairn Gorm during the months of November to February). Further, nearly 3000 body-mass readings were obtained from 89 individually marked birds visiting automatic electronic weighing balances. Winter body-mass showed a diurnal increase and was greater in males and birds with longer wings. Dawn body-mass peaked in late January, potentially allowing most birds to survive enforced fasts of more than 24 hours. Trapped birds were lighter during snowfalls. Adult females were generally heavier than juvenile females, and males averaged fatter than females. Experienced birds were seldom trapped, but comparison of trap masses and weighing balance masses indicated that these were heavier than naive individuals, and that unlike the latter, were capable of increasing in mass during bad weather. Birds at high altitude sites maintained higher energy reserves than those at coastal sites.

Finally, I investigated the influence of site experience, behavioural characteristics and energy reserves on side fidelity patterns of individually colour-marked Snow Buntings on Cairn Gorm. Males and experienced individuals were seen relatively more often during snow than before a snowfall, and adults more often than juveniles in snowfalls during early winter. Sex was more important early in the winter or during deep or prolonged snow. The probability that newly trapped birds would become established at the site was greater if they were males, or if they had above-average body-masses. Return rates to Cairn Gorm between winters increased with the number of times a bird was seen at the site in the first winter, but the return rates of birds seen often did not depend on either age, experience or dominance status. Males, however, were more likely

to return than females.

Snowfalls reduce the availabilty of Snow Bunting food supplies and probably force birds to use smaller feeding patches in greater densities (when aggression was shown to increase). Males, experienced birds and adults (despite an apparently lower dominance rank) were more efficient foragers in such circumstances, and this to some extent was reflected in their patterns of energy balance, as indicated by body-mass. Females and juveniles were hence less likely to become established at high altitude sites, while females and inexperienced individuals were less able to stay there in hard weather. This was reflected in the overall patterns of age/sex use of sites of different altitudes. Juveniles or inexperienced birds may show greater dominance than their counterparts because resources are relatively more important to them. Itinerancy, and lack of pair-bonding behaviour in winter, may have allowed adult and experienced Snow Buntings to reduce costs associated with aggression without completely undermining their ability to find sufficient food.

Chapter 1: INTRODUCTION

1.1 Social organisation and winter site choice

A key determinant of the biological viability or fitness (i.e. the contribution that particular types of individuals make to future gene pools) of seasonally-breeding birds is the ability to survive between breeding seasons (Newton 1989). Breeding constraints may not apply during this period and therefore a migration between breeding and wintering areas will occur if this increases the likelihood of survival and future breeding attempts. Within the wintering range there may be considerable variation between the quality of potential habitats, and their value may differ according to the requirements of the individual (see reviews by Partridge 1978, Goss Custard & Durell 1990). Potential site quality will mainly be determined by food availability and predictability, predation risk, presence or absence of conspecifics or other competitors, or costs involved in migration to the site. However, individuals will differ in their ability to realise a site's potential due to variability in their proficiency at such skills as feeding, competing and interacting with others, or avoiding predators. Ultimately these skills are mainly influenced by such individual attributes as age and experience, sex, body-size, and the presence of special trophic or agonistic adaptations (see reviews in Gauthreaux 1978, 1988, Partridge & Green 1985, Burger 1988, Marchetti & Price 1989).

Thus different individuals may achieve their maximum likelihood of overwinter survival in different habitats or areas. This association between individual attributes and the ability to realise a site's potential, provides one good explanation of why we often find intraspecific variation in migration distance from the breeding areas, or dispersal amongst alternative wintering habitats. Usually different categories of individual (e.g. age or sex classes) are found in different areas and/or habitats (reviewed in Gauthreaux 1982, Ketterson & Nolan 1983).

Individuals should therefore attempt to maximise their fitness by choosing a non-breeding site compatible with their attributes and abilities (Sutherland & Parker 1985). However, site choice is complicated by imperfect knowledge of the environment, or by unpredictable changes in the day-to-day quality of the environment or social conditions. Further, similar fitness pay-offs may be reached in different ways: e.g. by living as a dominant in a group of subordinates in poor quality habitat, or by being a subordinate amongst relatively more dominant individuals in high quality habitat. The fitness of different site choice and behavioural tactics will also depend on the frequency with which other individuals pursue the same or alternative tactics (see Lundberg 1987).

A degree of stability and predictability is introduced into the social organisation of many species by the *defense* of an area or a set of resources. Individuals or small groups of birds are *territorial*, preventing conspecifics from using and depleting food or other resources in a given area. They therefore benefit

because they can conserve sufficient resources for their own exclusive use, hopefully to last throughout the non-breeding season (Pulliam & Millikan 1982). They suffer, however, from time and risk costs involved in establishing and defending the territory (e.g. Davies 1976, Davies & Houston 1984). Competition for territories or for higher ranks within group territorial systems can be severe. However, the consequences of obtaining poor territories or low ranks on territories, or not obtaining territorial status at all, may be worse (e.g. Ekman *et al.* 1981, Rappole *et al.* 1989). Dispersal to neighbouring areas at times of food shortage may be impossible due to the territorial behaviour of other individuals or groups in such areas (e.g. in many tit species, Ekman 1989).

Other species are similarly sedentary in winter but exhibit a less rigid territorial system. In these species, individuals still benefit from being resident because this in itself confers a dominance advantage and hence priority of access to resources (e.g. Harris' Sparrows ☼☼, Rohwer 1977; Dark-eyed Juncos, Ketterson 1979a; Magpie, Eden 1987, Dhindsa *et al.* 1989). Piper & Wiley (1989) and Oberski & Wilson (1991) have even shown that dominance fluctuates throughout the home range of White-throated Sparrows and Great Tits respectively, with a peak around an individual's centre of activity. In these species, it should still be advantageous to remain faithful to a wintering site because movement to a new site would result in loss of dominance rank (e.g. Balph 1979).

Many of the most valuable studies of aspects of the behavioural ecology of wintering birds have been carried out on such sedentary species. Individuals can be found, trapped, resighted and retrapped in the field on a regular basis if necessary, and lack of success in finding birds can be assumed, with a reasonable degree of confidence, to indicate that they have died. Furthermore, these species are often ideal for aviary study because dispersal (i.e. beyond the boundaries of the territory or cage) is not considered to be an option that they would frequently resort to. Thus experimental manipulations generally leave the birds with a similar range of behavioural options as they would have in field situations. There is therefore an extensive and detailed literature on many aspects of the behaviour and ecology of several species which are sedentary in winter (see some outstanding examples in **Table 1.1**). Such studies, amongst others, have now provided strong evidence that attributes of wintering/non-breeding birds, such as age, sex, size or prior site experience mould aspects of their behaviour, notably their foraging and agonistic behaviour. Dominance or a high level of feeding efficiency are often equated with bird quality, partly because in some analyses these have been shown to affect patterns of change of body-mass or individual survival.

☼☼ All scientific names of species referred to by their English names in the text can be found in an appendix to this thesis.

Table 1.1. An illustration of the wide variety of behavioural and ecological studies carried out on a group territorial species (Willow Tit), and two sedentary flocking species (Dark-eyed Junco and White-throated Sparrow) in winter. *Letters refer to species-specific studies listed below the table.*

	Willow Tit	White-throated Sparrow	Dark-eyed Junco
Age vs dominance	GKM	CG	GQR
Sex vs dominance	GK	CD	G
Age/sex vs winter distribution	A	D	KU
Age/sex vs winter mass		E	
Age/sex vs foraging	GHI		
Age/sex vs survival	BDJ		JU
Size vs dominance	M	CK	G
Dominance vs prior site experience	KM	CDK	QRS
Dominance vs winter distribution	C	D	BP
Dominance vs winter mass	L	EG	T
Dominance vs foraging	GHL	BFJ	IM
Dominance vs survival	CDI	E	BE
Dominance vs aggression	K	H	HV
Aggression vs winter conditions			CF
Aggression vs population composition	K		G
Aggression vs flock-size			D
Winter mass vs prior site experience		E	
Winter mass vs survival		E	
Winter mass vs winter conditions		A	A
Foraging vs winter conditions	GH		NO
Foraging vs flock-size	F	I	
Foraging vs survival	EI		
Winter distribution vs survival	ACD		JU

Willow Tit: Ekman 1979, A; 1984, B; 1990, C; Ekman *et al.* 1981, D; Jansson *et al.* 1981, E; Hogstad 1988a, F; 1988b, G; 1988c, H; 1988d, I; 1989a, J; 1989b, K; Ekman & Lilliendahl 1993, L; Koivula *et al.* 1993, M.

White-throated Sparrow: Blem & Shelor 1986, A; Schneider 1984, B; Piper & Wiley 1989, C; 1990a, D; 1990b, E; Piper 1990, F; Wagner & Gauthreaux 1990, G; Archawaranon *et al.* 1991, H; Pearson 1991, I; Wiley 1991, J; Dearborn & Wiley 1993, K.

Dark-eyed Junco: Helms & Drury 1960, A; Fretwell 1969, B; Pulliam *et al.* 1974, C; Balph 1977, D; Baker & Fox 1978, E; Ketterson 1978, F; 1979a, G; 1979b, H; Baker *et al.* 1981, I; Ketterson & Nolan 1982, J; 1983, K; 1985, L; Theimer 1987, M; Lima 1988a, N; 1988b, O; Rogers *et al.* 1989, P; Cristol *et al.* 1990, Q; Holberton *et al.* 1990, R; Wiley 1990, S; Cristol 1992, T; Swanson 1992, U; Ramenofsky *et al.* 1992, V.

Many studies of these and other species with restricted home ranges in winter (e.g. King *et al.* 1965, Nisbet & Medway 1972, Goss-Custard 1976, Smith 1976, 1984, Goss-Custard *et al.* 1984, Lundberg 1985, Owen & Dix 1986, Adriansen & Dhondt 1990, Ornat & Greenberg 1990) have looked at how individuals distribute themselves, either over large areas or within territories or habitats. The winter distribution is often relatively stable once it has been established in early winter. Alternatively, predictable changes in population distribution and composition may occur as the winter progresses (e.g Goss-Custard *et al.* 1984, Duncan & Marquiss 1993). Another group of species exist, however, which, as evidenced by erratic fluctuations in numbers, and perhaps movements of ringed birds, are generally considered to be much more mobile. Such species are usually associated with unpredictable food supplies such as tree seeds or rodents (Newton 1972, Andersson 1980, Bekoff & Scott 1989) or food supplies which become inaccessible as a result of severe weather conditions (Evans 1981, Fuller 1986, Green 1986).

Much less is known about the winter behavioural ecology of these more mobile species, especially at the level of the *individual*. Some *populations* are known to exhibit differential migration (e.g Kerlinger & Lein 1986, Prescott 1991), with younger and/or smaller birds tending to travel further than their counterparts. Social and environmental factors affecting feeding and aggression rates have been looked at within flocks of plovers (Barnard & Thompson 1985), and thrushes (Barnard & Stephens 1983), but without considering individual attributes such as age, sex or social dominance. Dominance relationships among age/sex categories, and some factors affecting aggression rates are known amongst irruptive Evening Grosbeaks (Bekoff & Scott 1989). Productive studies have also been made of mass levels and roosting site choice in relation to age and sex in Bramblings, a species which can disperse rapidly in response to the abundance (production) and accessibility (due to snowfalls) of Beech mast (Jenni & Jenni-Eiermann 1987, Jenni 1993).

However, apart from Bekoff & Scott's (1989) observations of the low rates of aggression amongst Evening Grosbeaks and their discussion of the implications this has for promoting social foraging, only the work of Senar and his co-workers on the Siskin has examined the factors causing some birds to become sedentary whilst others are nomadic. In some outstanding field and aviary studies of this species they have shown the importance to transients of seeing or hearing other birds feeding, and the willingness of residents to be joined (local enhancement), the higher status of residents compared to dominants, a high frequency with which dominants defer to subordinates, a lower rate and intensity of fighting amongst dominants or birds which are familiar with each other, and greater masses of residents compared to transients (Senar & Metcalfe 1988, Senar *et al.* 1989, 1990a,b, 1992a). Only 8% of birds became resident even when excess food was continuously available. Interestingly, transients also have more pointed wings, generally considered to make flight more energy-efficient (Senar *et al.* 1994). This suggests that individuals may be pre-programmed to either a transient or resident lifestyle. The lack of age and sex differences between resident and transient Siskins supports this idea further (Senar *et al.* 1992a). The lower masses of transients may therefore be due to active regulation of body reserves rather than to food deprivation, because carrying

excess mass may be inefficient. Senar *et al.* (1989, 1990a,b) also describe how the social organisation and social interactions between dominants and subordinates might promote flock cohesion and stability, lending more support to the possibility that both dominants and subordinates (residents and transients) benefit from the stategy that they adopt (the shepherds hypothesis, see also Rohwer & Ewald 1981). Furthermore, this flock cohesion and winter pair-bond formation (Senar 1985, Senar & Copette 1990) may help explain the lack of any segregation of the age and sex groups in winter (Payevsky 1994). Unfortunately, as with many other mobile species, the lack of either direct or indirect data on fitness or survival of different types of birds is disappointing but inevitable.

At the onset of periods of low food availability or bad weather, mobile species can decide whether to abandon their present site in search of a more favourable area or remain where they are and trust that they have sufficient energy reserves to last until feeding conditions ameliorate. Moving away might be costly since a more profitable site may not be found, information about food sources and mortality risks will have to be relearned, and existing dominance hierarchies may limit access to preferred feeding sites. On the other hand, remaining at a deteriorating site or delaying a move elsewhere could hasten starvation. The choice of whether or when to move may be as critical as the original choice of wintering site, and may similarly vary intraspecifically, depending on an individual's existing energy reserves and how its knowledge, expertise and agonistic ability are likely to limit its future access to food in degenerating conditions.

Therefore, a rigorous investigation of the mechanisms involved in site choice and future movement patterns requires analysis at the level of the individual. Studies of the costs and benefits of individuals adopting different strategies have yielded many useful insights in other fields of ecology (e.g. the influence of optimal foraging theories on dietary analyses, Stephens & Krebs 1986), and would allow interpretation of intraspecific variation in movement patterns. However, this approach has not so far been attempted in mobile species because of the difficulties of relocating birds on a regular basis.

During the winter of 1987/88 I had the opportunity to catch and mark Snow Buntings at several inland sites in North-east Scotland. I found that numbers fluctuated at each of my sites and that total numbers caught exceeded maxima seen. Moreover, some birds were caught at the same site over long periods, but others moved to different sites 25km or more from where I originally caught them. References to other wintering Snow Bunting populations indicated that such fluctuations and movements were not unusual. In March 1988, I therefore began to individually colour-ring them at one site, and began to study fidelity to this site by marked individuals. The implications of having a fluctuating population of birds encompassing a mixture of strategies from transients to residents soon became clear. I therefore attempted to make more detailed behavioural and ecological observations of this species at my inland sites over the next few winters.

1.2 Biology of the Snow Bunting

Snow Buntings are typical medium to large Emberizid finches which are sexually dimorphic in summer (males predominantly black and white, females grey or brown and white), but more similar in winter when grey or brown feather tips conceal the nuptial plumage. Males, however, can still be readily distinguished from females at this time, particularly in flight, by the size of the species' main distinguishing features: large white patches on the inner wings and outer tail. On average, males are up to 10% larger in linear dimensions than females (Banks *et al.* 1989).

They breed in many open habitats throughout the Arctic, providing there is some vegetation where they can feed, and cavities (amongst boulders, cliffs, or buildings) in which to nest. Territories are dispersed across the tundra, and in many places they are the commonest breeding bird. They are typically monogamous, and, as a result of the brevity of the Arctic summer, usually single-brooded, leaving the breeding areas soon after the autumn moult period (Nethersole-Thompson 1966, Alerstam 1990, Smith & Marquiss in press a,b). They then move up to several thousand kilometres southwards, to winter on the plains and coasts of North America, Asia and Europe (Nethersole-Thompson 1966, Zink 1985, Alerstam 1990). In some southern parts of the breeding range, such as Iceland and Scotland, the winter climate is less severe and the breeding and wintering ranges overlap (Nethersole-Thompson 1966, Alerstam 1990). Some southern breeding populations (e.g. that in Iceland) may be only partial or local migrants (Breuil 1989). In western Europe, largely south of the breeding range, the wintering population is biased towards females (reviewed by Banks *et al.* 1991a), suggesting males from the breeding populations involved are more sedentary or move shorter distances south.

In the non-breeding season Snow Buntings become gregarious, ground-feeding birds of open country. The diet changes from mainly invertebrates in summer, to mainly vegetable matter in autumn and winter, although they will continue to take invertebrates when these are available (Nethersole-Thompson 1966, Watson 1966, Lambert 1986). The seeds of herbaceous plants, particularly grasses, sedges and rushes comprise the bulk of their winter diet. They are frequently found on farmland, taking cereal grains and perhaps other weed seeds in stubble fields. They are also quick to exploit other sources of food provided by man, and may become very tame (Nethersole-Thompson 1966, Watson 1977, pers. obs.). These characteristics make them particularly easy to attract to bait and trap (Nethersole-Thompson 1966, Rae 1986).

In Britain, Snow Buntings are predominantly winter migrants. They are usually found in flocks of between 5 and 200 birds, and occur in a variety of open habitats at all altitudes from the seashore and estuaries, sand-dunes and dune slacks, to farmland and moors. They are also frequently seen on the tops of even our highest mountains. The altitudinal variation of their wintering locations simulates north-south climatic and habitat gradients in north-west Europe.

Plumage characteristics and ringing recoveries suggest that about 80% of Snow Buntings wintering in Britain are of the Icelandic race *insulae*, with smaller numbers of the similar-sized nominate race *nivalis* from Greenland and/or Scandinavia (Banks *et al.* 1991a, Smith in prep.). Although a breeding population does exist on Scotland's hills, it is small (presently estimated at 50-100 pairs - Watson & Smith 1991, Smith 1993), and is swamped by large numbers of winter immigrants (10,000-15,000 birds; Lambert 1986).

The itinerant nature of wintering Snow Buntings is suggested by several observations that numbers fluctuate greatly between and within winters at specific sites in Britain (e.g. Williamson 1966, Lambert 1986, Banks *et al.* 1991b). Banks *et al.* (1991b) also reported that many more birds were caught at ringing sites in North Scotland than were ever seen, that the proportion of birds which were ringed remained constantly low during the winter despite further trappings, and that less than 5% of birds were proven to return to the sites where they were originally ringed in subsequent winters. Nomadic tendencies are further implied by some exceptional ringing recoveries, notably a bird of probable Greenland origin that was trapped and retrapped on successive spring migrations in Scotland and Newfoundland (see review of Snow Bunting movements by Williamson 1966). Prys-Jones (1984) considered that high mobility, or close association with man, were essential strategies for ground-feeding passerines wintering in regions regularly combining sub-zero temperatures and high precipitation - snowfalls can rapidly render food supplies unavailable in such climates. He suggested that Snow Buntings were the best example of such a mobile species and quoted Dementiev & Gladkov's (1954) observations of birds on the Russian Steppes: "...the concentration of wintering [Snow Buntings] on any given locality may vary sharply depending on the abundance of snow".

Severe conditions occur frequently in Scotland in winter, especially in upland regions. The mobility of Snow Bunting populations in response to food unavailability should be particularly marked in montane areas due to the greater frequency and size of snowfalls. Individuals may frequently have to decide whether changes in snow-cover warrant movement elsewhere. The rapid transition (in terms of distance) from montane to arable and coastal environments in North-east Scotland gives birds the option of escaping some bouts of bad weather by moving a relatively short distance to lower ground. Conversely, there is potential to return to high altitude sites as soon as these again become favourable. The Snow Bunting populations of North-east Scotland therefore seem to be potentially good subjects in which to study site choice and movement decisions.

1.3 Aims of this study

The main purpose of this project was to gather detailed behavioural and ecological data from individuals of a highly mobile, non-territorial passerine, allowing comparisons with the many excellent works carried out on sedentary species at the opposite end of the spectrum. Perhaps because of the very nature of the project and the species studied, the approach was almost entirely observational, as opposed to experimental. The

following chapters are largely a presentation and interpretation of these observations.

The first aim was to establish whether general patterns of Snow Bunting site use occur in North-east Scotland, particularly with respect to age and sex. The *altitudinal* difference between habitat types, resembling the *latitudinal* distribution of similar habitat types, offered an opportunity to test whether or not higher (and by implication more northerly) wintering sites were preferred by Snow Buntings, without the confounding influence of migration distance differences between sites (for mechanisms see Gauthreaux 1978, 1982, Myers 1981a,b, Ketterson & Nolan 1982, 1983).

Next, I show the influence that weather conditions have on changes of Snow Bunting numbers and population composition at an upland site. I attempt to interpret this in relation to the patterns of movements that have been observed between my upland sites and elsewhere.

I then report on the foraging and agonistic behaviour of Snow Buntings to establish which individual attributes affect performance. Environmental and social influences on performance are also examined. In the light of some unusual dominance relationships between different categories of birds, I describe the characteristics and consequences of aggressive interactions in some detail.

Mass change may reflect the success of individuals in obtaining sufficient energy resources to minimise the probability of starvation. I therefore look at how time of year, weather and wintering site affect the levels of reserves that individuals maintain, and determine whether there is variation between different types of bird.

Finally, I attempt to draw all these strands together by looking, at how individual attributes, aggressive behaviour, and levels of energy reserves affect a Snow Bunting's likelihood of becoming established at a site, staying at that site, and returning there in future non-breeding seasons.

Chapter 2: STUDY AREA, WEATHER and GENERAL METHODS

2.1 Cairn Gorm Study Area

Almost all observations of marked birds and recording of behaviour was carried out on Cairn Gorm, in the central Scottish Highlands, on an area of about 6km² of open hill and montane habitat between about 500m and 1100m above sea level (**Fig.2.1**). This area, subsequently referred to as the Ski Area, hosts a large ski resort and its associated development (ski tows, chairlifts, access road to 630m, and four groups of service buildings). The vegetation succeeds from peatlands and Heather moorland at low levels, to prostrate Heather, then *Empetrum* and *Racometrium* heaths, and finally *Juncus trifidus* heaths at high altitudes. There are many areas of boulders or naturally bare/scantily vegetated ground. The high, steep and convoluted nature of the terrain traps snow in natural corries and gullies, and this has been enhanced by artificial means (bull-dozing of trenches and snow-fencing). Access and artificial encouragement of snow-lie have inevitably led to erosion and many areas have been reseeded in an attempt to minimise the visual impact of the damage. Such erosion and reseedings may not, however, be detrimental to Snow Buntings, because birds were often seen feeding on such areas.

The Ski Area was split into three altitude bands (**Fig.2.1**) which, to some extent, represented natural divisions of my labour due to access arrangements. Level 1, from 500-650m a.s.l., was accessible by car, and was the main level used for behavioural observations and trapping. Three baited areas, chosen because they could be observed from a car, were provided at Level 1, at the Ciste Feeding Station (CIFS), Ciste Bait (CIB) and Cas Car Park Bait (CCPB). Birds were trapped at all three baited areas, but not at CIFS after April 1988. I hoped that Snow Buntings would then recognise that CIFS was a safe feeding site, and that even the most trapshy individuals (see **5.3.2**) would visit it. Behavioural observations, particularly of feeding rates, and automatic mass registrations, were concentrated at this site. Baited areas were not essential to bring Snow Buntings down to Level 1. They were frequently seen feeding on natural vegetation at this altitude, but also alongside roadside embankments, at two sites where Reindeer were frequently fed, and on scraps dropped by skiers in the car parks.

Level 2 extended from 650-850m a.s.l. and mainly comprised the area of the Day Lodge Tow (where occasionally bait was provided and birds trapped if they would not descend to lower levels - see **5.3.4**), and the area above the Shieling. Occasionally observations were made at Level 2 if there were few birds at Level 1, and Level 3 was inaccessible.

Level 3, between 850m and 1100m a.s.l., was in most parts very steep and often too dangerous (due to ice and high winds) to ascend on foot. Nevertheless, Snow Buntings were frequently seen at these altitudes, especially when the snow-line was high (see **5.3.4**). I mainly visited Level 3 in winter periods with little

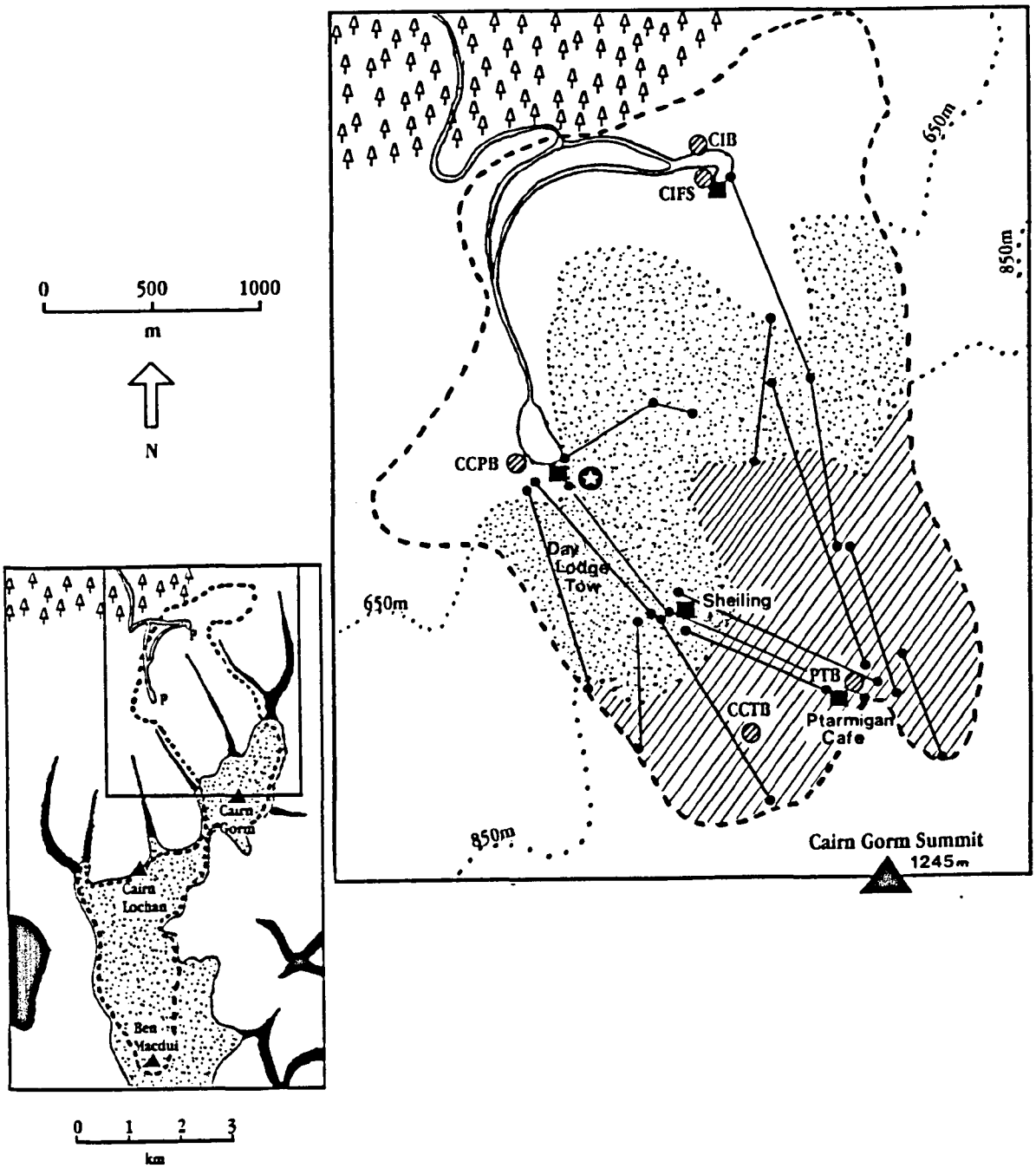


Fig.2.1. Maps of the Cairn Gorm study area. *The lower map shows the extent of the entire area within the Cairngorm Mountains, or Cairngorms, in which winter observations were made (enclosed by dashed line) in relation to the extent of the adjacent montane ground (above 900m; light shading) and forested areas. Darker shading indicates other ridges and areas of high ground. 'P' represents major car parks.*
The inset is reproduced above in more detail and shows the boundaries of the Ski Area (dashed line). Contours separate altitude zones 1-3 within the Ski Area: Level 3 is indicated by the darkest shading, Level 2 is paler, whilst Level 1 has no shading. Straight lines indicate ski tows; boxes are major service buildings. My catching and observation sites are indicated by hatched circles (for names see text). The star indicates the location of the weather station monitored by Cairngorm Ranger Service (see 2.3). Level 4 is the high ground south of the Ski Area, and is bounded by the dashed line on the lower map, excluding the Ski Area (upper map).

snow-cover, and when such conditions persisted (see **Fig.2.3**) I provided bait at Coire Cas Tow Bait (CCTB) and/or Ptarmigan Bait (PTB). These sites were chosen because they provided me with essential shelter in the form of buildings and snow fences/cairns. Inevitably, however, they were rather public. Snow Buntings were seen feeding over almost all of Level 3, in a variety of natural and semi-natural vegetation types, as well as on scraps at the 1080m Ptarmigan Cafe.

In addition to observations made on the Ski Area, I also occasionally looked for Snow Buntings on approximately 10km² of the adjacent montane plateau, a National Nature Reserve ranging from 1000m to 1309m a.s.l. (**Fig.2.1**). This area, referred to as Level 4, was mostly visited in very mild conditions, or in periods of high pressure when both safe access was possible, and Snow Buntings could not be found on the Ski Area. Bait was only provided on Level 4, at the summit of Ben Macdui, during one short, very mild spell in late January/early February 1992.

2.2 Other trapping sites

I established baited areas at four other upland sites in North-east Scotland (Glen Shee, The Lecht, Corgarff and The Cabrach; **Fig.2.2**) in winter 1987/88. These sites were all known to have held wintering Snow Buntings in the past. I trapped birds at each of these sites in 1987/88, and continued to provide bait and trap at two of the sites, Glen Shee and The Lecht, until winter 1992/93.

Glen Shee and The Lecht are both high altitude ski resorts, chosen for their road access to high ground as well as the known presence of Snow Buntings. Glen Shee boasted the highest regular trapping site (660m), but the surrounding hills were lower, on average, than those on Cairn Gorm (highest point within 5km was 1070m). Glen Shee is also greener, richer and less rugged than Cairn Gorm, although areas of boulders and bare ground can be found at higher elevations. The Lecht is lower still (catching site 630m, highest point 800m), and sits amongst rolling Heather moorlands and peatlands rather than the montane habitat of Cairn Gorm and Glen Shee.

The site at Corgarff was only 4km from The Lecht, but was 230m lower in altitude. The general area comprises marginal hill farmland bordering Heather moorland, with some plantation forestry. Snow Buntings were found and baited in a field where (unusually) oats had been cut and left as stooks, before being threshed in the field. However, birds, including marked individuals, were also seen in other fields nearby. The Cabrach was again marginal hill farmland, but lower than Corgarff (catching site at 340m), with less access to high ground (highest point 630m). Large (100+) flocks of Snow Buntings were observed using a wide variety of fields at The Cabrach prior to provision of bait.

In addition to trapping data from these sites, I was able to get trapping data for the winters of 1987/88 and 1988/89 from six other sites, courtesy of members of Grampian and Highland Ringing Groups . Five of

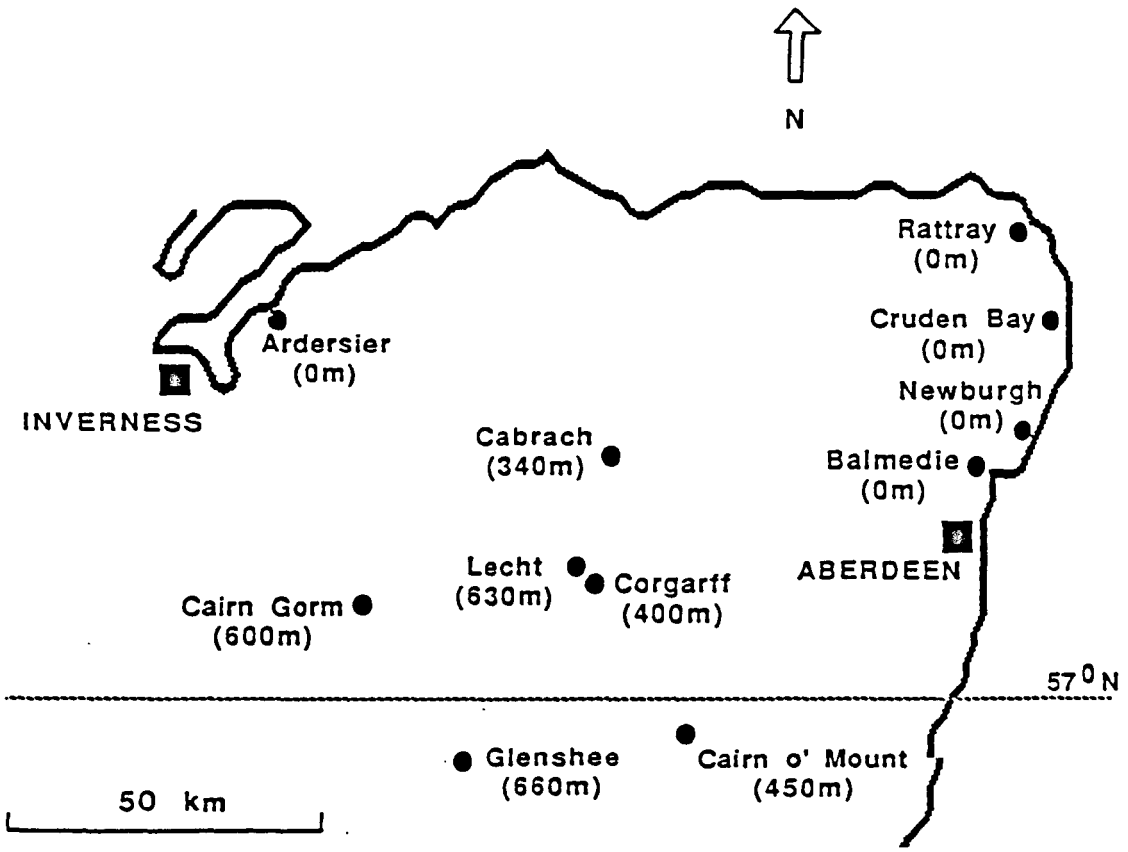


Fig.2.2. Location and altitude of Snow Bunting trapping sites (filled circles) in North-east Scotland.

these sites were coastal (**Fig.2.2**), but the Cairn o' Mount site was a rolling medium-altitude Heather moorland (catching site at 450m, but highest point only 520m). One of the coastal sites was in farmland, but the others were adjacent to the sea in sand-dunes or dune slacks. Snow Buntings in coastal habitats were commonly seen foraging along the shoreline, or in the dune systems themselves.

2.3 Measurement of weather variables

Daily weather observations were made by Cairngorm Ranger Service at a weather station at 670m in the middle of the Cairn Gorm Ski Area (see **Fig.2.1**). The weather station was visited at approximately 9a.m. each day, although visits were occasionally delayed or made impossible by severe weather conditions. The ranger service recorded current wind speed and direction, current temperature, minimum and maximum daily temperatures, amount of precipitation, average depth of snow below the weather station, and ground conditions/snow cover. Maximum temperature was entered retrospectively (i.e. 24 hours late) because the maximum daily temperature was likely to have occurred after 9a.m. I then derived the following variables which were thought likely to be of importance to wintering Snow Buntings because they could have affected ground foraging and/or thermoregulation:

i) 9AM TEMPERATURE to the nearest Celsius.

ii) Mean daily temperature (MEAN TEMPERATURE) to the nearest Celsius. This was the arithmetic mean of the minimum and maximum daily temperatures.

iii) Mean WIND SPEED in miles per hour, the average of the range of readings observed when the reading was taken.

iv) SNOW DEPTH in cm.

v) SNOW COVER. This was a categorical estimate of the proportion of ground covered by snow or ice, based upon a more detailed range of possible ground conditions recorded by the ranger service (mainly dryness/dampness of open ground or type of snow). SNOW COVER was defined by me as 0 if there was no snow or ice, and the ground was not frozen; 1, if the ground was frozen, ice-covered, or with partial snow cover; and 2, when snow cover was complete.

Precipitation was not used *per se* because on many days snow was not melted to obtain a daily reading.

These five variables are referred to throughout the text. 9AM and MEAN TEMPERATURE, and WIND SPEED were approximately normally distributed, allowing me to use their absolute values in parametric tests. However, the absolute value of SNOW DEPTH was used only in non-parametric tests. SNOW COVER was only used as a categorical variable. The values of each variable were grouped for other analyses. The groupings may differ between tests, in order to provide suitable sample sizes.

In some analyses, I also looked for relationships between my results and the previous day's weather, or combinations of present and previous weather. Throughout this thesis such variables are given an

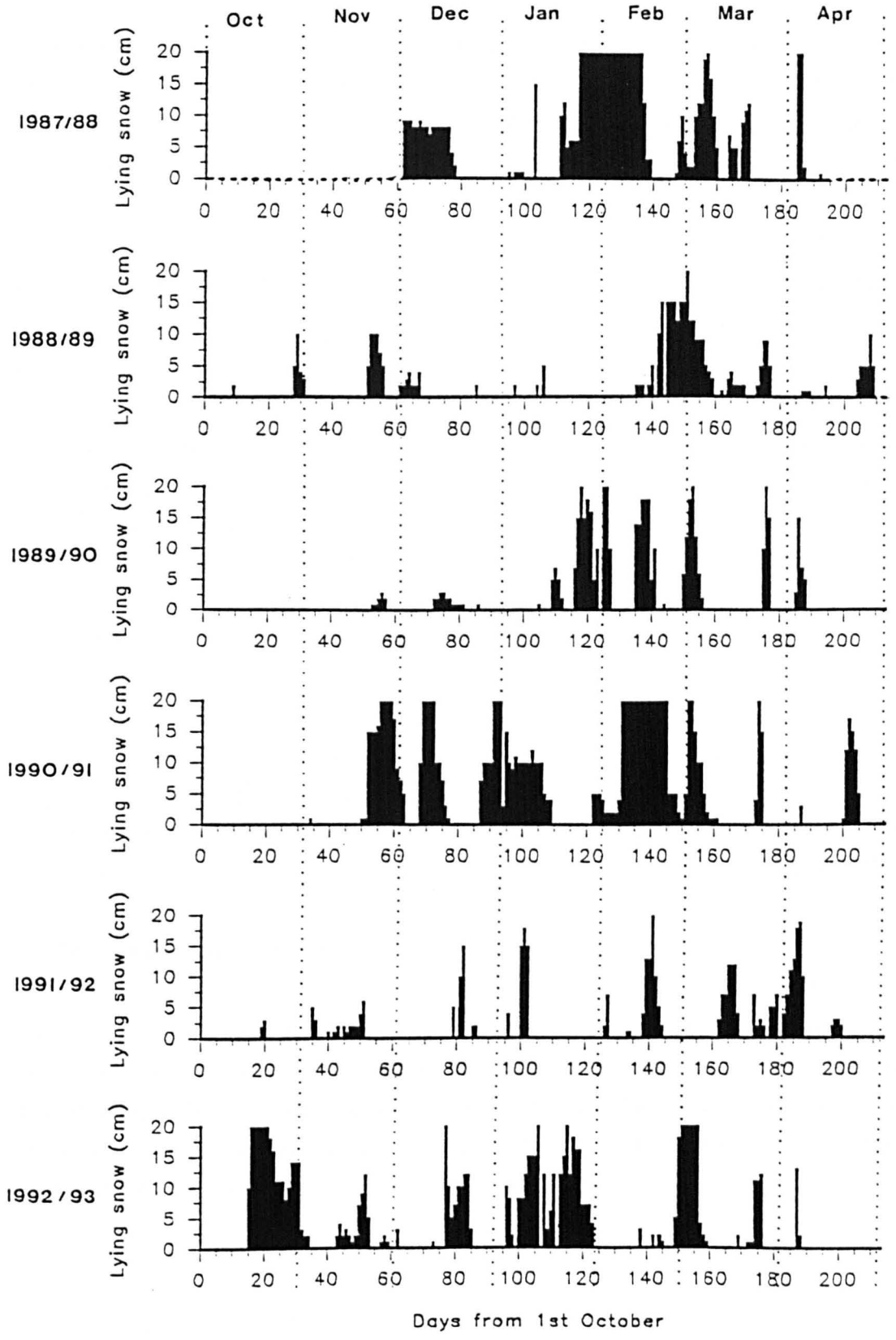


Fig.2.3. The depth and duration of snow-cover at the Cairngorm Ranger Service's weather station at 670m on Cairn Gorm during the study winters. *Broken lines on the horizontal axis indicate periods during 1987/88 when no data were available. Smaller snowfalls have been over-emphasised by representing all snowfalls of 20cm or more as 20cm - the maximum recorded depth was 64cm.*

appropriate and descriptive suffix. For example, 9AM TEMPERATURE PREVIOUS DAY refers to the previous day's temperature at 9a.m, WIND SPEED (2-DAY MEAN) refers to the mean of WIND SPEEDs on the present and previous days, and SNOW DEPTH (8-DAY MEAN) refers to the mean of the grouped values of snow depth on the present day and previous seven days.

Another potentially important variable was CONSECUTIVE DAYS SNOW COVER, the number of successive days of at least partial snow cover at the weather station (i.e. SNOW COVER was either 1 or 2). I excluded the current day in this calculation, and defined a maximum upper limit to the variable of five days consecutive snow cover.

In addition to the weather variables generated from the Cairngorm weather station, I also received (from the Meteorological Office) daily records of the altitude above which there was more than 50% snow-cover (referred to as the 50% snow-cover line). This measurement is still made using imperial units (in 500-foot bands, starting at 1000ft), explaining the rather awkward metric conversions used in this thesis. The readings were taken from Aviemore, looking approximately 12km south-east at the northern side of the Cairngorm Mountains, and, as such, included my main study site on Cairn Gorm.

The winters during the main study period (1987/88 to 1992/93) were variable but generally mild (Adam Watson and Cairngorm Chairlift Company, pers.comm.). **Fig.2.3** shows the length and extent of snowfalls on Cairn Gorm during each winter, whilst **Table 2.1** shows the number of days each winter with MEAN TEMPERATURE below freezing, greater than 50% snow-cover above 914m (3000ft) and less than 50% snow cover even above 1219m (4000ft). 1988/89 and 1991/92 were particularly mild and snow-free.

2.4 Definition of a snowfall

A snowfall, or snow bout, was defined as a period where at least 5cm-days of snow was lying at the Cairngorm Weather Station at 670m. Therefore, 1cm of snow for 5 or more days, or 5+cm on one or more days constituted snowfalls, whereas falls of, for example, 1cm for 4 days, 2cm for 2 days, or 4cm on only one day were ignored. I defined the end of the snowfall as the first day that snow was not present at the weather station.

Table 2.1. Temperature and snow-lie patterns on Cairn Gorm during the study winters.

	% of days in November to February with:		
	MEAN TEMPERATURE below 0°C	50% snow-cover line below 914m	50% snow-cover line above 1219m
1987/88 a	52	95	2
1988/89	16	50	41
1989/90	25	82	10
1990/91	42	86	4
1991/92	16	46	48
1992/93	28	72	22

a **Results based on data for January & February only.**

2.5 Trapping and marking techniques

Snow Buntings were attracted to areas which were baited regularly with grain (oats or barley), oatmeal or biscuit crumbs. Bait was provided almost daily on Cairn Gorm, but more erratically elsewhere (approximately weekly, but sufficient amounts to last for several days). All birds handled were caught using elastic-propelled 'whoosh' nets (see Davis 1981, Rae 1986). These are manually fired, giving the trapper complete freedom to choose when to release the net over the baited area. However, individual Snow Buntings become shy of areas where they are whoosh-netted frequently (Rae 1986, see also **5.3.2**). They then tended to feed peripherally (where they were less prone to capture), when the net was not present, or avoided the trapping area completely. I therefore left dummy equipment in place at all times, although experienced individuals still appeared to know whether or not they could feed without risk of capture.

Catches were therefore biased towards birds which had little experience of the trapping site (**5.3.3**). However, the primary purpose of trapping was to handle and mark as many birds as possible. Hence, to reduce the speed with which birds became trapshy (anxiety amongst experienced individuals appeared to spread to naive birds), I avoided firing on small numbers of birds, or on groups with a high proportion of birds which had been marked previously.

After firing the net, I bagged the whole catch individually or in pairs before commencing to mark and measure them. All birds were marked with individually numbered metal leg rings, and up to three darvic colour-rings. The latter weighed just over 0.04g, and in combination with the 0.07g metal ring were equivalent to less than 0.7% of the mass of even the lightest individuals. The colours (nine available), number and relative position of the rings allowed me to subsequently identify individuals or their ringing sites during field observations (as opposed to recatching them). Since February 1988, all Snow Buntings captured on Cairn Gorm received individual combinations of three colour-rings. At the other sites, usually only one or two colour-rings were applied to newly caught birds. This was still sufficient to indicate when (which winter) and where the bird was marked. If a site/year marked bird was seen away from its original ringing site, I attempted to recapture it and give it extra colour-rings in order to be able to identify it individually and monitor its subsequent settlement and movement patterns (**5.3.6**).

Although ageing and sexing techniques for Snow Buntings were known before this work began (Svensson 1984), discussions with Robert Rae indicated that better techniques were available. These were further developed and are presented in **3.5**. Almost all birds handled were therefore sexed, and the vast majority (96%) could also be aged with confidence. Wing-length, body-mass, fat score and various plumage measurements were also noted (see **3.2** & **8.2.1**). Birds were released individually or in small groups, generally within 30-90 minutes of capture.

2.6 Winter immigrants and local breeding birds

A small Scottish breeding population of Snow Buntings, currently numbering between about 50 and 100 pairs (Smith 1993) exists on Scotland's highest hills. Such a small population would be of little significance here, if the main breeding area in the central and western Cairngorm Mountains (up to 40 pairs, Smith *et al.* 1993) did not neighbour my main winter study area (Cairn Gorm). Luckily, I have also been able to observe, trap and mark many of the Snow Buntings in the Cairngorms during the summers 1988 to 1993 (see summaries of work in Smith 1991, 1993, 1994, Smith & Marquiss in press a,b, Smith *et al.* 1993). Birds were defined as being of local origin if they were originally ringed on the Scottish breeding grounds (as chicks, early autumn juveniles or breeding adults) or ringed in winter but seen on the breeding grounds in summer. They are henceforth referred to as local breeders. I probably identified most birds of local origin as local breeders because:

i) at least 80% of the territorial birds within 50km of any of the catching sites were checked for rings each summer (Smith & Marquiss in press b), and

ii) most of their chicks were ringed.

Local breeders were more frequent on Cairn Gorm than at other sites. Generally 5-8 individuals, almost always males, remained for long periods on Cairn Gorm each winter. They usually formed a small minority of the birds seen each day. Occasionally other males and a few females were seen for shorter spells, mostly during milder weather or during spring (Smith 1994). Where appropriate, local breeders were removed

from the analyses.

Otherwise, all birds visiting the wintering sites were assumed to have come from breeding grounds outwith Scotland (mainly Iceland - see **1.2**). They are referred to hereafter as winter immigrants.

2.7 Juveniles and adults

Throughout this thesis birds in their first year of life are termed juveniles. During their first breeding season, when 10-14 months old, I refer to them as first-summer birds. Thereafter they are termed adults. Only a small proportion of trapped birds could not be aged with certainty (see **3.3.1**). These were omitted from analyses which compared age categories.

2.8 The non-breeding season

In North-east Scotland, Snow Buntings begin to lay eggs in mid- to late May, and may still be attending their young in mid-August. Few winter immigrants are seen after the first few days of May, and few probably return in autumn much before mid-October (unpubl. data, Thom 1986).

Winter immigrant Snow Buntings were generally first seen at low altitudes on the Ski Area in November, although large flocks were sometimes seen at higher altitudes from mid-October. They were still commonly seen on the Ski Area until late April, although many departed during March (see **8.3.12a**). Throughout this thesis, I use the terms 'non-breeding season' and 'winter' to refer to the period between about November and April. In many analyses, data were selected or grouped according to three 2-month periods during the non-breeding season, namely (i) Early Winter (November and December), (ii) Mid Winter (January and February), and (iii) Spring (March and April). As birds fattened and departed during Spring, it was often necessary to discard data collected during this period.

2.9 Statistical treatment

Most statistical analyses were conducted using the SPSS/PC+ package (Norusis 1986a,b). All probabilities given are two-tailed. Yates' correction was applied to all chi-square tests with one degree of freedom. Combined Probability Tests were carried out using the method described by Sokal & Rohlf (1981).

Chapter 3: AGE DETERMINATION, WING-FEATHER COLOUR AND WING-LENGTH CHANGE

This chapter was originally published in 'Ringing & Migration' in 1992, and is presented here in a style close to that text:

Smith, R.D. 1992. Age determination, wing-feather colour and wing-length change in Snow Buntings. Ring. & Migr. 13: 43-51.

3.1 INTRODUCTION

Innovations in catching methods (see Rae 1986) have led to a substantial increase in the number of Snow Buntings trapped in Britain in recent winters. Standard age/sexing criteria (Svensson 1984) proved unreliable in Scotland, probably due to the high proportion of the Icelandic race *P.n. insulae* found there (Rae & Marquiss 1989, Banks *et al.* 1990, 1991a). Svensson (1984) makes no distinction between races, but his descriptions seem to fit the nominate race better than *P.n. insulae*. This encouraged ringers to look for new methods and consequent publications revising age/sexing criteria have followed (Rae & Marquiss 1989, Banks *et al.* 1990). However, these have still noted difficulties in determining the age of some birds from plumage characteristics or outer tail-feather shape (Rae & Marquiss 1989, Banks *et al.* 1989), limiting the scope of further analyses. Rae & Marquiss (1989) did, however, suggest that tertial wear and colouration may be a reliable indicator of age. The first aims of this chapter are therefore to present further evidence in support of this method, to introduce an additional criterion based on greater covert wear, and to modify methods of age determination based on tail-feather shape and wear.

Additionally, the success of these methods is tested by looking for differences in wing-feather colour and wing-length in Snow Buntings aged as juveniles or adults. Differences in wing-feather colour may arise as a result of delayed plumage maturation, a phenomenon already reported in this species and many other passerines (Rohwer & Butcher 1988). Juvenile passerines have also been commonly reported as having shorter wings than older conspecifics. This is often attributed to either nutritional constraints when the feathers are growing, or their role in increasing flight manoeuvrability (for examples and discussion see Alatalo *et al.* 1984). Snow Buntings retain their juvenile flight feathers throughout their first winter (Svensson 1984; pers. obs.). Differences in feather colour and/or wing-length between age categories would therefore support the accuracy of my ageing criteria.

3.2 METHODS

I handled 2188 Snow Buntings at five inland sites in North-East Scotland during the four winters 1987/88 to 1990/91. Birds were trapped between late November and late April at areas baited with grain, and were thought to be of mainly Icelandic origin based on ringing recoveries and plumage characteristics (Banks *et al.* 1990; **5.3.6**). They were sexed mainly on the extent of black in the lesser and median coverts (Banks *et al.* 1990). Some adult females and juvenile males, however, overlapped using this criterion but were usually easily recognised once aged. Only two individuals could not be assigned to a sex category: both were aged as juveniles and were thought to be either unusually well-marked females or very dull males. One of these was subsequently retrapped the following winter as an obviously adult male.

Ageing techniques are outlined in the Appendix to this chapter. These were devised not only from information collected from the large sample of individuals handled (and retrappings in subsequent winters), but also from plumage characteristics of 56 birds trapped during their post-juvenile moult on the Scottish breeding areas. Birds were assigned to one of three age categories (adult, juvenile or unknown) based on whether the three groups of feathers considered were fresh, worn or intermediate respectively (but see Appendix for exceptions).

The extent of white on the wings was measured by estimating by eye the percentage of white on each flight-feather of the right wing to the nearest 5%. Only that portion of the feather not hidden by the coverts was considered. This method gave consistent results when the same bird was measured more than once in the same winter (mean difference between estimates of the amount of white in the variable second innermost primary in within-winter recaptures was 2.5%, maximum 15%, n=65). On some birds, particularly adult males, some white was visible on all six secondaries and nine primaries. The individual percentages of white on each feather were summed to obtain an overall wing-patch score. Although the size of each feather differs (and so the area of white represented by a particular percentage will vary between feathers), the pattern of white was similar between birds, decreasing outwards and inwards from the second and third innermost secondaries (see Fig.1 in Rae & Marquiss 1989). Therefore wing-patch score, although not directly proportional to the area of white in the wings, should still be strongly related to it. Wing-patch change was calculated for birds caught in two consecutive winters by subtracting wing-patch score in the first winter from that in the second and expressing this value as a percentage of the wing-patch score in the first of the two winters. Large positive values (maximum observed=106%) therefore represent an increase in wing-patch score (i.e. more white) between winters, while values close to zero indicate little difference between winters.

Average wing-length measurements (maximum chord, to the nearest mm) for individual age and sex categories only include measurements from the first winter in which a bird was trapped. Repeat measurements from individuals recaptured in subsequent winters are analysed separately. A few birds had

severely abraded or broken their longest primary tips and so were not measured.

3.3 RESULTS

3.3.1 Evidence for reliability of age determination

Over the course of the four winters 95.8% of new birds trapped were conclusively assigned to an age category (i.e. either juvenile or adult) and this increased each winter from 93% in 1987/88 to 99% in 1990/91. This occurred to some extent because my experience of, and confidence in, the ageing criteria increased, but also because I first began to record the pattern of renewal and abrasion of the inner greater coverts in 1988/89. Recaptures of individuals ringed in or before the previous winter indicated that the method successfully determined the ages of known adults (**Table 3.1**). This applied equally to adults first ringed as nestlings (2% of retrapped sample), juveniles (47%), and adults (51%). **Table 3.1** also indicates that the ageing criteria were similarly successful in determining the ages of known juveniles.

The consistency of the method was measured by examining the 514 within-winter retraps where an individual had been conclusively aged on consecutive occasions. Only one bird was misclassified, suggesting that the method gave consistent results, at least within observers.

Table 3.1. Age classification on recapture of Snow Buntings of known age.

	Aged as:		
Ringing period	Adult	Juvenile	Unknown
Previous winter or before			
- known adult	145	0	1
Previous summer (nestling)			
- known juvenile	0	7	0
Previous summer (juvenile)			
- known juvenile	0	2	0

On the whole, ageing of individual feather groups based on wear conformed to my overall assessment of a bird's age (**Table 3.2**). However, the proportion of birds whose feathers complied with their overall age classification changed during the course of the winter. Juveniles generally appeared less abraded early in the winter, while adults, especially males, often looked very worn in spring. These problems were often overcome by considering the colour of the feathers in question as well as their abrasion (see Appendix). The proportions of the three feather groups of known adults (retrapped from previous winters) which were fresh/worn were similar to those of birds classed as adults on first capture.

3.3.2 Amount of white on the flight-feathers

Wing-patch score of Snow Buntings aged as juveniles on first capture was greater in their second winter, particularly if the extent of the white wing-patch was relatively small in the first winter (**Fig.3.1**; females, r_{16}=-0.91, P<0.001; males, r_{34}=-0.85, P<0.001). However, in birds aged as adults on first capture no relationship was noted between change in wing-patch score and wing-patch score in the first of the two winters (**Fig.3.1**; females, r_{24}=-0.36, P=0.08; males, r_{18}=0.35, P=0.14). Nor were wing-patch scores significantly different between the two winters (paired t-tests: females, t_{25}=0.50, P=0.62; males, t_{19}=0.30, P=0.77).

3.3.3 Wing-length change

Within the 1989/90 winter, the wing-lengths of 62 Snow Buntings were measured on more than one occasion. Six birds had longer wing-lengths when remeasured, 12 were shorter and 44 were unchanged. On average they lost 0.085mm per 100 days, not significantly different from the null hypothesis of no abrasion. Therefore no correction was made for abrasion during the course of the winter.

Average wing-lengths for the four age/sex categories in each of the four winters are given in **Table 3.3**. There were no significant differences in wing-length between winters for any of the age/sex categories, but adults were in every case significantly longer-winged than juveniles.

Furthermore, I compared the wing-lengths of 105 individuals for which data were available from two consecutive winters (**Fig.3.2**). Amongst birds aged as juveniles on first capture, females showed an average increase of 1.16mm between winters (t_{19}=2.61, P=0.02) and males an increase of 1.68mm (t_{33}=7.08, P<0.001). Those aged as adults on first capture showed a slight but non-significant increase in wing-length the following winter (t_{48}=1.69, P=0.1). It might be argued that this increase was due to mis-classification of some juveniles as adults. However, if some birds were misclassified, wing-patch score should also have increased in the following winter. This was not the case: I could find no relationship between change in wing-patch score and change in wing-length among adults where both measurements were made in both winters (females: r_{23}=0.14, P=0.49; males: r_{18}=-0.11, P=0.66).

Table 3.2. The percentage of birds assigned to each age/sex category in three winter periods whose inner greater coverts, longest tertials, and central tail feathers agreed/disagreed (n) with their overall age classification based on feather wear. *Percentages do not add up to 100% because in some cases the feather groups could not be conclusively aged. Sample sizes differ between feather groups, because in some birds the relevant feathers were wet or missing. 'All' refers to whether or not the three feather groups unanimously agreed/disagreed with the age classification.*

Ageing method	November-December	January-February	March-April	All months
Juvenile female				
Inner greater coverts	90/ 7 (61)	90/ 5 (61)	91/ 5 (171)	91/ 5 (292)
Longest tertial	80/ 0 (61)	90/ 0 (61)	95/ 1 (172)	92/ 1 (293)
Central tail-feathers	87/ 4 (54)	95/ 4 (56)	94/ 2 (162)	93/ 3 (272)
All	76/ 0 (54)	80/ 0 (56)	86/ 1 (161)	83/ 0 (271)
Juvenile male				
Inner greater coverts	84/ 4 (51)	100/ 0 (44)	98/ 2 (44)	94/ 2 (139)
Longest tertial	80/ 8 (51)	95/ 0 (43)	98/ 0 (44)	90/ 3 (138)
Central tail-feathers	90/ 0 (50)	95/ 0 (39)	100/ 0 (43)	95/ 0 (132)
All	70/ 0 (50)	95/ 0 (39)	95/ 0 (43)	86/ 0 (132)
Adult female				
Inner greater coverts	96/ 0 (132)	92/ 2 (106)	92/ 0 (79)	94/ 1 (317)
Longest tertial	95/ 0 (132)	89/ 2 (105)	80/ 6 (78)	89/ 2 (315)
Central tail-feathers	92/ 1 (117)	90/ 4 (95)	83/ 4 (69)	89/ 3 (281)
All	90/ 0 (117)	83/ 0 (94)	74/ 0 (68)	84/ 0 (279)
Adult male				
Inner greater coverts	85/ 3 (59)	75/10 (63)	52/28 (29)	74/11 (151)
Longest tertial	95/ 0 (59)	92/ 2 (64)	63/13 (30)	88/ 3 (153)
Central tail-feathers	98/ 0 (53)	93/ 0 (55)	36/41 (22)	85/ 7 (130)
All	83/ 0 (53)	76/ 0 (54)	24/10 (21)	70/ 2 (128)

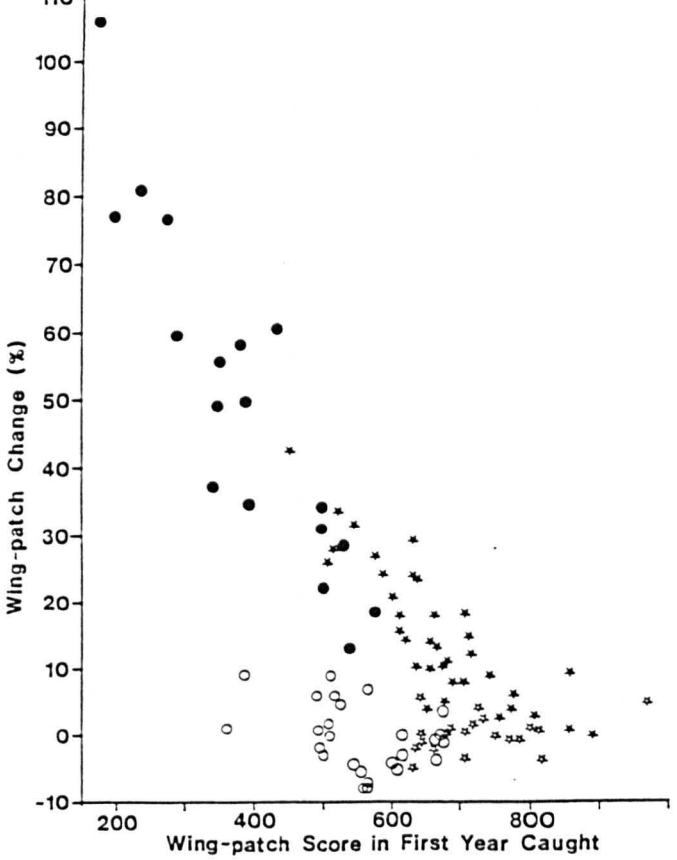


Fig.3.1. Percentage change in Snow Bunting wing-patch score (a measure of the extent of white on the wings) between two consecutive winters versus wing-patch score in the first of these winters. *Birds classified as juvenile females in the first winter trapped are shown by solid circles, juvenile males are solid stars, adult females are open circles and adult males are open stars.*

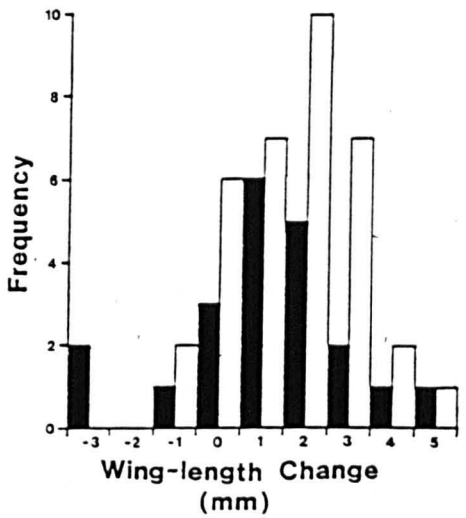


Fig.3.2. Frequency of wing-length change (mm) between the first and second winters of individual Snow Buntings. *Positive values indicate an increase in wing-length in the second winter, negative values a decrease. Solid bars represent females, open bars males.*

Table 3.3. Wing-lengths (mm) of Snow Buntings trapped in inland North-east Scotland from 1987/88 to 1990/91 in relation to age and sex.

		Mean wing-length ± s.d. (n)		
		juveniles	adults	P
Females	1987/88	105.45 ± 2.19 (275)	106.51 ± 2.32 (163)	***
	1988/89	105.58 ± 2.05 (258)	106.33 ± 2.34 (173)	***
	1989/90	105.44 ± 2.18 (118)	106.66 ± 2.22 (248)	***
	1990/91	105.85 ± 2.15 (33)	106.83 ± 2.29 (127)	*
	Σ	105.51 ± 2.15 (684)	106.57 ± 2.29 (711)	***
	Range	99-113	99-113	
Males	1987/88	111.63 ± 2.10 (156)	112.90 ± 2.32 (84)	***
	1988/89	111.68 ± 2.14 (110)	113.44 ± 1.96 (72)	***
	1989/90	111.57 ± 2.03 (84)	113.65 ± 2.35 (86)	***
	1990/91	111.77 ± 2.59 (28)	113.13 ± 2.89 (58)	*
	Σ	111.64 ± 2.13 (378)	113.29 ± 2.38 (300)	***
	Range	107-119	105-121	

*** = P<0.001, * = P<0.05 (two-tailed t-test)

3.4 DISCUSSION

This chapter provides evidence that the method of ageing Snow Buntings using longest tertial wear (Rae & Marquiss 1989) is reliable. It also describes and tests two other methods for separating juvenile Snow Buntings from older birds and finds these equally useful. Although Snow Buntings wintering on the study sites largely showed characteristics of the Icelandic race *P.n. insulae*, the method also seemed to extend to the paler nominate race: pale females and white-rumped males, typical of the *nivalis* subspecies, were as readily aged using the methods described as darker *insulae* types. The success of these methods divorces the ageing process from the need to consider the colour of the greater and primary coverts (Svensson 1984), a method prone to misinterpretation due to individual and racial variation. Feather wear, especially on the inner greater coverts and tertials, can also be used to age birds in the field (see 6.2).

The extent of the white wing-patch of juvenile and adult Snow Buntings overlaps extensively (**Fig.3.1**), but extreme values may help age difficult individuals. The wing-patches are conspicuously displayed by both sexes during courtship (Tinbergen 1939; pers.obs.), and hence may influence mate choice. It is not clear, however, when juveniles may benefit from having smaller wing-patches than adults. To help answer this question, it would be useful to know when birds replace lost wing-feathers with adult- rather than juvenile-type feathers. If juvenile-type feathers are only regrown for a short time after fledging, crypsis at this time may be the driving force behind delayed plumage maturation. Juvenile-type feathers may still be regrown during the subsequent winter if it is advantageous to accurately signal age (and hence, perhaps, low competitive ability) in winter flocks (see Rohwer & Butcher 1988). Alternatively juvenile males may regrow juvenile-type feathers until the following summer because it helps them look more like females, thus possibly reducing aggression from adult males (reviewed by Lyon & Montgomerie 1986). Replacement with adult-type feathers may be more likely when sexual selection advantages outweigh such hypothesized benefits. Female mimicry seems an unlikely explanation, however, because *both* sexes exhibit a delay in attaining full wing-feather colouration. Experimental removal of single wing-feathers from juveniles (consequently inducing feather regrowth) could help elucidate the time-scale over which juvenile plumage is the better fitness option. Such an experiment would be most successful if carried out on dull juveniles since these show the most marked change from juvenile to adult-type feathers.

The increases in wing-length between winters of birds originally trapped as juveniles (**Fig.3.2**) were very similar to the differences between means of the overall sample (**Table 3.3**), and therefore provide strong evidence that the ageing criteria were correct. However, the difference in mean wing-length between juvenile and adult Snow Buntings in my study area could, in isolation, also be interpreted as differential mortality or fidelity of birds of different wing-lengths. The similar results obtained from both types of analyses, along with the lack of evidence for decreased wing-length variation with age (standard deviations of juvenile and adult wing-lengths were similar, **Table 3.3**), therefore suggests that, within age and sex categories, wing-length does not influence mortality or site fidelity.

Age can have a powerful influence on a bird's behaviour, ecology, and morphometrics (see, for example, discussions by Alatalo *et al.* 1984, Burger 1988, Gauthreaux 1988) and should be considered, whenever possible, in analyses comparing and contrasting differences between individuals. Ambiguous ageing criteria may, however, easily hide real differences between age categories. Such confusion may have prevented previous studies of Snow Buntings from finding significant differences between adult and juvenile wing-lengths (Banks *et al.* 1989, Rae & Marquiss 1989). The present study clearly shows that such a difference does exist and can be detected even with small sample sizes.

3.5 APPENDIX: Age determination

Three sets of feathers (**Fig.3.3**) were found to be useful indicators of age irrespective of sex and race, and

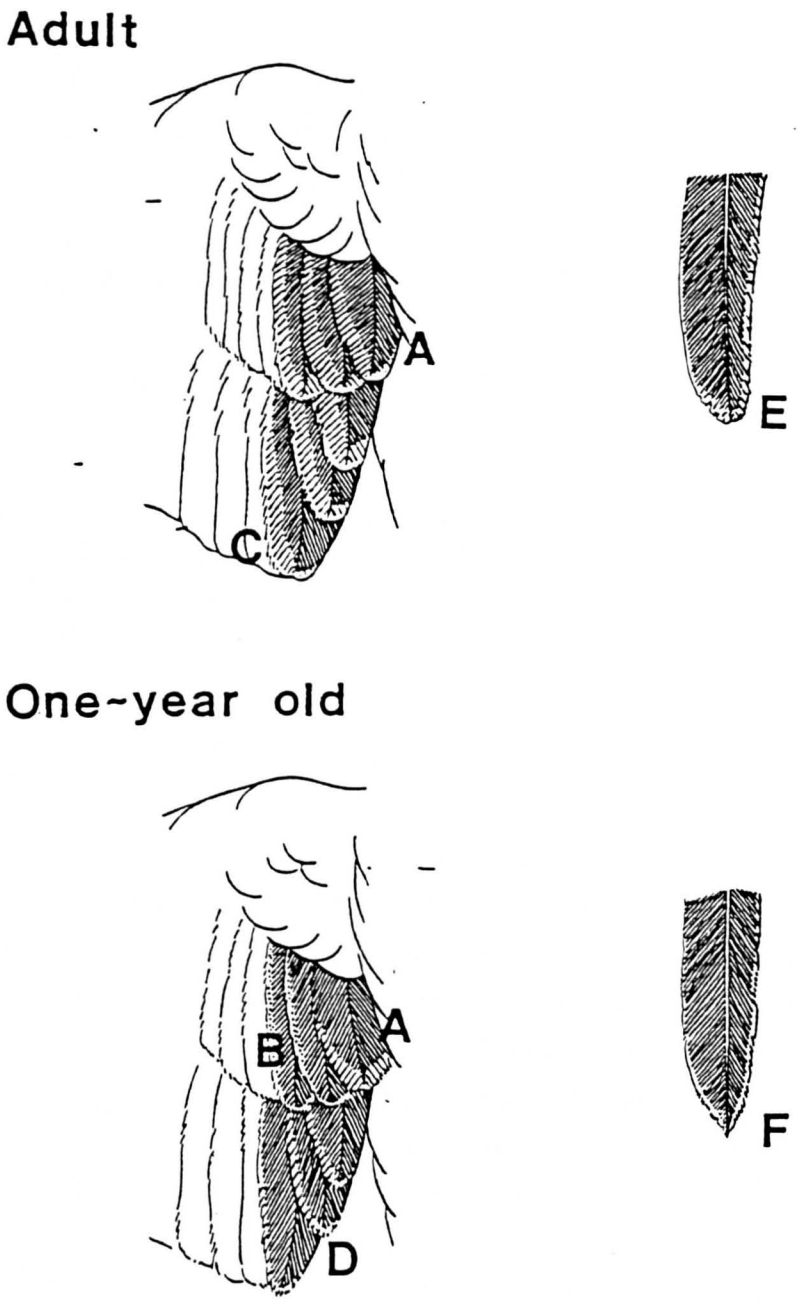


Fig.3.3. The inner greater coverts, tertials and central tail feathers of typical adult (above) and juvenile (below) Snow Buntings in North-east Scotland. *Other feathers are not shaded. A-F refer to ageing criteria developed in the appendix.*

should apply from October to early May. They are outlined with precedence given to the criteria most likely to give a true indication of age although all points should be checked if possible.

The easiest and most reliable method of identifying juveniles is to look for a contrast between the first and second innermost greater coverts which, if present, is unequivocal. The new adult-type feather (A in **Fig.3.3**) is broadly tipped and edged (>2mm) ginger with males often also having an obvious white streak between this margin and the dark inner part of the feather. Juvenile-type inner greater coverts, retained from the plumage as a nestling, are initially also ginger-edged but by December most have worn to a duller and narrower margin (B). Few juvenile birds replace more than one or two greater covert, but if none are moulted confusion can arise with occasional faded/abraded adults.

Tertial colour and wear, particularly on the longest feather, shows a similar pattern to the inner greater coverts. Adult feathers are broadly edged ginger, especially on the outer edge of the tip where the margin may be up to 5mm wide (C). Retained juvenile feathers are similar in the autumn although slightly less ginger, but become worn by November to give a dull brown margin rarely more than 2mm wide (D). The shape is also modified by wear to give a more pointed and narrower feather than that of adults. The tertials are rarely moulted and hence no contrast is seen between old and new feathers as in the greater coverts, but wear becomes less obvious on the smaller, less exposed tertials.

Finally, the central tail feathers (rather than the second and third outermost feathers advocated by Svensson 1984 which seem to be more variable) can be useful indicators of age, although caution is necessary if the feathers become wet or soiled. I have no reason to suspect that natural tail feather loss is a common occurrence in winter and have never observed moult of the rectrices in autumn juveniles. Therefore misclassification of juveniles as adults on this basis will be infrequent. Adults have rounded central tail feathers with a paler tip (E), often enclosing a dark extension of the shaft. Abrasion, even when prominent, generally leaves a rounded appearance to the tips of adult tail feathers. In juveniles, the paler tip wears more quickly, resulting in a more pointed and narrower feather with obvious abrasion (F).

The main exceptions to these patterns appear to be adult males, particularly pale individuals, from late winter onwards. These rapidly lose the pale feather fringes and can look very worn as the bird attains its summer plumage. However, the subterminal pale bands on the inner greater coverts and on the less worn shorter tertials are usually still present.

Abrasion seems to become more rapid from May onwards and breeding birds handled in summer (after early June) were not easily aged using the above methods. The amount of white in other plumage tracts, combined with knowledge of the race involved, may then give better results.

Chapter 4: AGE AND SEX VARIATION IN CHOICE OF WINTERING SITE: THE EFFECT OF ALTITUDE

This chapter was originally published in 'Ardea' in 1993, and is presented here in a style close to that text:

Smith, R.D., Marquiss, M., Rae, R. & Metcalfe, N.B. 1993. Age and sex variation in choice of wintering site by Snow Buntings: the effect of altitude. Ardea 81: 47-52.

4.1 INTRODUCTION

The choice of wintering sites by migratory birds will have important consequences for overwinter survival and/or subsequent reproduction. However, individuals will differ in their ability to survive at wintering sites due to variation in experience (i.e. accumulation of skills such as foraging, fighting or predator avoidance) or physiological characteristics (e.g. variation in body size or insulation). This variability should lead to a non-random assortment of individuals over a winter range; older, more experienced birds (review in Gauthreaux 1988) and larger, more competitive birds (reviews in Gauthreaux 1978 and Ketterson 1979a) will be least limited in their choice of wintering sites. I refer to sites preferentially occupied by such birds as high quality or optimal sites, and those avoided as being of low quality or sub-optimal.

The most familiar evidence for non-random distribution of individuals over a winter range is latitudinal segregation of age or sex categories (for reviews see Gauthreaux 1982, Ketterson & Nolan 1983). Adult birds and those of the larger sex (usually males) tend to winter nearer the breeding grounds. Gauthreaux (1978) presents a model predicting that such distributions can be explained by the costs of migration (i.e. disadvantages of increasing migration distance). The model also predicts that dominant birds will be commoner in favoured habitats. This suggests to me that an alternative explanation for the latitudinal segregation of age or sex categories could be that habitat quality increases towards the breeding grounds. Explanations of latitudinal segregation have largely ignored the latitudinal distribution of sites of differing quality. However, if sites nearer to the breeding grounds are of higher quality, it will be difficult to separate the relative influences of migration costs and habitat quality on site choice.

Wintering populations of the Snow Bunting show a bias towards females in more southerly wintering areas (Banks *et al.* 1991a). In this chapter, I examine the age and sex composition of populations at sites that are relatively close together, but in a range of habitats at varying altitudes. This altitudinal gradient is similar to latitudinal gradients in that both higher altitude and more northerly sites will have a more severe climate and less predictable food supply for ground-feeding birds such as Snow Buntings, due to fluctuations in snow and ice cover. However, the gradients also share several possible compensations: for example, competitors or predators are likely to be less abundant. I test my suggestion that habitat quality is an

important determinant of site choice, and is higher nearer to the breeding grounds, by looking for selection of high altitude (and, by connotation, high latitude) sites by the most competitively able age and sex categories of wintering Snow Buntings. If this were the case, I predict that adults (more experienced) and males (larger and dominant) will be proportionately more frequent at high altitudes. In contrast, if the proportion of adults or males does not vary between sites, or is skewed towards low altitude sites, this would be good circumstantial evidence that migratory distance is an over-riding parameter affecting the preponderance of males in the north.

4.2 METHODS

Snow Buntings were trapped and ringed using similar techniques at 11 baited sites (five of mine, six others run by local bird-ringers - see **2.1 & 2.2**) in North-east Scotland during the winters of 1987/88 and 1988/89 (**Fig.4.1**). I am confident that competition for access to these baited sites was not affected by altitude since there was no relationship between site altitude and either the maximum count of Snow Buntings at a site or the total number of birds trapped at a site. Similarly, neither the maximum count nor the total sample affected the proportions of each age/sex category trapped at a site (all $P>0.15$).

Birds were caught by six trappers each of whom aged and sexed birds using techniques described by Rae & Marquiss (1989), Banks *et al.* (1990) and **3.5**. The small proportion of captures (4.1%) which could not be confidently assigned to an age category are not considered further. Consistency was improved amongst five of the six trappers by attending some catches together. The sixth trapper caught Snow Buntings at a coastal site without comparing his age/sex assessments with the other trappers. To assess the affects of inter-trapper differences four of the five, along with the sixth, independently aged and sexed a series of 26 winter Snow Bunting skins obtained in North-east Scotland. Only two trappers disagreed about the sex of single skins, proving our sexing technique consistent. However, ageing was more variable with only 14 birds agreed unanimously. The four trappers who had made catches together aged 5, 5, 6 and 8 skins as adults, whilst the isolated trapper aged 11 skins as adults. The estimated proportion of adult birds at his coastal site may therefore have been higher than if one of the other trappers had caught there. However, adjusting for this would merely serve to strengthen the results and conclusions of this chapter and so no corrections were made.

The eleven winter trapping sites fell within a circle of radius 70km (**Fig.4.1**) and were therefore relatively close together in comparison to the distances that Snow Buntings travelled from their breeding areas in Iceland, Greenland and Scandinavia (1000-2000km). Distance from the breeding grounds could still be a confounding variable, however, if significant numbers of Scottish breeding birds were present at one or more of my wintering sites. However, the Scottish breeding population is small and likely to be swamped by large numbers of winter immigrants (see **2.6**). Moreover, in the summers of 1988 and 1989 almost 80% of the breeding territories (n=51) known to hold birds in any of the previous summers since 1970 (locations

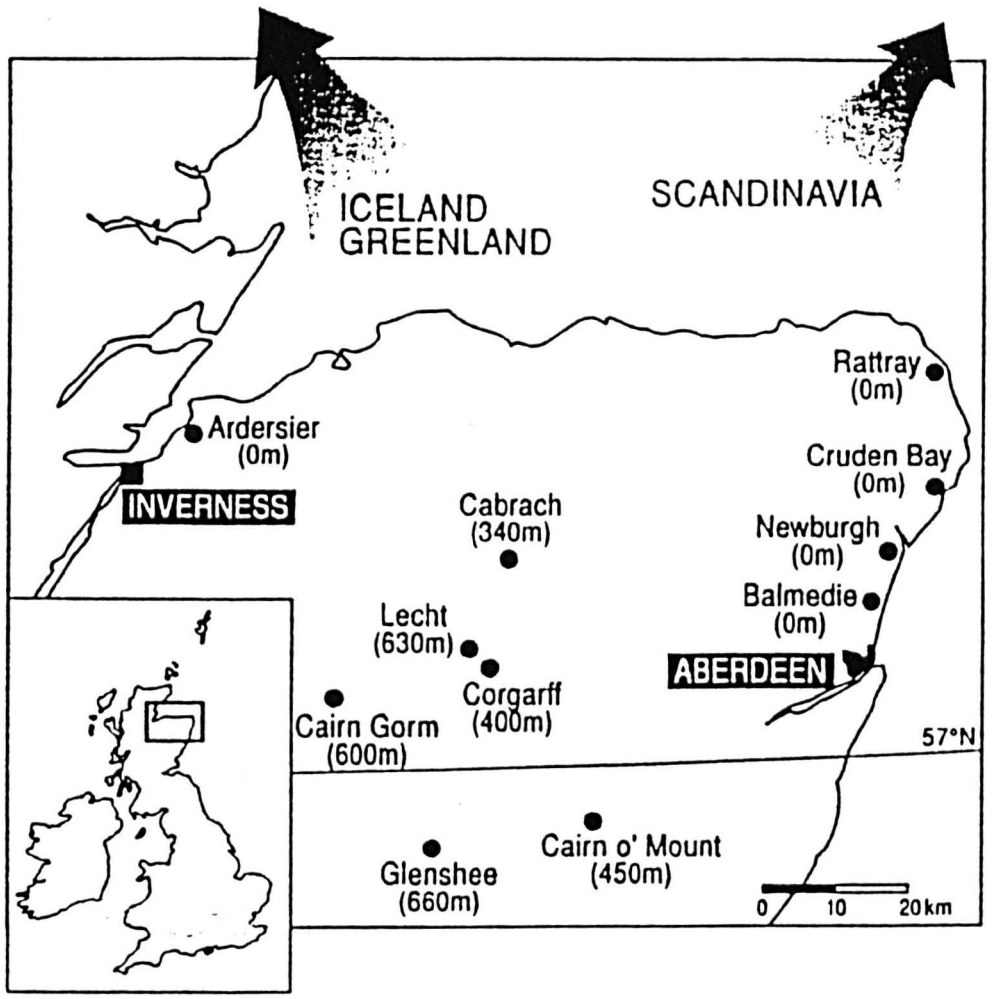


Fig.4.1. Location and altitude of Snow Bunting trapping sites in North-east Scotland in relation to the direction of breeding areas in Greenland, Iceland and Scandinavia.

of territories summarised in Watson & Smith 1991) were checked. Nineteen winter-ringed adults were found and these were removed from all analyses.

Only the first capture of an individual at a given site in each calendar month was considered in analyses of the population composition; the first capture in each subsequent month was also included in the analyses as a retrap. I controlled for possible seasonal movements by specific age and/or sex categories by sub-dividing the winter into three periods (Early Winter = the total number of captures in November and December, Mid Winter = January-February, Spring = March-April). I have only used data points based on more than 20 captures.

Altogether a total of 3309 captures remained for analysis. Approximately equal numbers of birds were caught at inland and coastal sites in each winter (1987/88: inland - n=764, coastal - n=923; 1988/89: inland - n=790, coastal - n=832). 10.8% of captures were retraps (2.5% between winters, 8.3% within winters). Despite the ensuing lack of independence, I report an analysis which included these retraps, to give the best estimate of overall age/sex composition. Discarding the retraps might bias the analysis towards transient birds. However, I obtained similar results if the same analysis was performed without including retraps.

I recorded four habitat variables at each site:

i) Altitude (m a.s.l.) of trapping site.

ii) Altitude (m a.s.l.) of highest point within 5 km; this is less arbitrary than trapping site altitude because a considerable range of altitudes within a small area may be used by Snow Buntings on a daily basis (see **5.3.4**).

iii) Distance (km) from the coast, an index of the effort required to fly to low ground in severe weather.

iv) Distance (km) from nearest known Scottish breeding site. This variable allowed inter-seasonal explanations of distribution to be considered, but should not be confused with direct territorial or site familiarity advantages. Instead, because all known Scottish breeding birds have been omitted from the analysis, this variable is justified due to a possible preference by winter immigrant Snow Buntings to winter in or near to habitat similar to suitable breeding habitat (rather than to reduced migration distances to these Scottish breeding areas).

The four variables were highly intercorrelated (all comparisons: minimum magnitude of $r=0.91$, $P<0.001$). I therefore used a Principal Components Analysis to extract a single component; this explained 95% of the variance in the site-related data, with loadings on the standardised variables as follows:

COMPONENT 1 = (0.97 x trapping site altitude) + (0.98 x highest point altitude) + (0.98 x distance to coast) - (0.96 x distance to suitable breeding habitat).

In North-east Scotland, sites with a high value of Component 1 will tend to be high montane areas and

regions with low values of Component 1 will be low ground near the coast. The component thus represents an altitudinal cline and will be referred to subsequently as Altitude.

I report here the results of four analyses of covariance which had the proportions of each age/sex category as the dependent variable and Altitude as the covariate. I corrected for seasonal variation by including period within the winter as a factor. Preliminary analyses indicated that annual variation was non-significant and negligible, and so I pooled the data from a site if it was available in both winters.

4.3 RESULTS

After correcting for seasonal variation, the proportion of juvenile females decreased with Altitude, whilst that of adult females and adult males increased with Altitude; there was no relationship between the proportion of juvenile males and Altitude **(Table 4.1)**.

Fig.4.2 illustrates this relationship for the Mid Winter period, when active migration should be least likely to affect the age/sex composition of birds at a site. The increase in proportion of adult males and decrease in proportion of juvenile females were significant for this period alone, as well as being significant over the entire winter **(Table 4.1)**.

4.4 DISCUSSION

The proportion of adult male and female Snow Buntings trapped in North-east Scotland increased with altitude, while the proportion of juvenile females declined. At the preferred wintering sites we would expect proportionately more dominant individuals, or more individuals better able to withstand the effects of competition through, for example, superior feeding techniques or local knowledge. Male Snow Buntings are significantly larger than females (Banks *et al.* 1989; **8.3.1**), win the majority of intersexual encounters (see **7.3.3**), and attain higher feeding rates than females in competitive situations (**6.3.2b**). Feeding rates are also higher in adult Snow Buntings (**6.3.2b**), perhaps as a result of greater competitive, foraging or site-related experience. Juvenile females and adult males, which showed the strongest relationships with Altitude in this analysis, are therefore probably at opposite ends of a spectrum of ability to winter at preferred sites in the face of intraspecific competition. The prevalence of adult males at high altitude sites then suggests that these are higher quality wintering areas. Furthermore, because the proportion of adult females also increases with altitude, but that of juvenile males does not, age and experience may have greater roles than size and dominance in determining an individual's ability to exist at a high altitude site.

Table 4.1. Analysis of covariance between the proportion of each age/sex category of Snow Buntings and Altitude in the three winter periods. *There were no significant interactions between winter period and Altitude (i.e. the slopes of the regressions of the proportion of each age/sex category on Altitude did not differ within the winter, all P>0.1). I present the significance of Altitude after adjusting for differences in the elevation of the regression lines within the winter if these elevations were significantly different. Otherwise the significance of the linear correlation is given.*

	Winter Period		Altitude		
Age/sex category	$F_{2,18}$	P	B a	t b	P
Juvenile female	5.13	0.017	-0.12	3.74	0.002
Adult female	0.93	n.s.	0.06	2.17	0.042
Juvenile male	1.71	n.s.	0.01	0.29	n.s.
Adult male	8.09	0.003	0.10	4.73	<0.001

a **Note that the slope, B, is based on the arcsine transformed proportion of each age/sex category.**

b **d.f. = 18 if t is the test statistic after adjusting for a significant effect of winter period, and 20 if winter period does not significantly affect the Altitude covariate: t then results from the simple linear regression.**

An increase in site quality with altitude might seem counterintuitive because birds wintering at more elevated sites will have to suffer a more rigorous climate than those in the coastal environment. On high montane sites, the greater metabolic cost of heat generation, and the higher risk of starvation due to periodic food unavailability (snow and ice covering natural food supplies) must be outweighed by some survival or fitness advantages for the inland wintering strategy to be viable. For example, when upland sites are snow-free they provide vast areas of open ground with short seed-producing vegetation. This food source is, moreover, largely unexploited by other birds - no other similar-sized granivores winter commonly above 600m a.s.l. in North-east Scotland (Buckland *et al.* 1990).

However, food biomass is unlikely to be the sole explanation for habitat segregation, due to its extreme unpredictability on the snow-prone montane sites. Preferential wintering at upland sites could also be

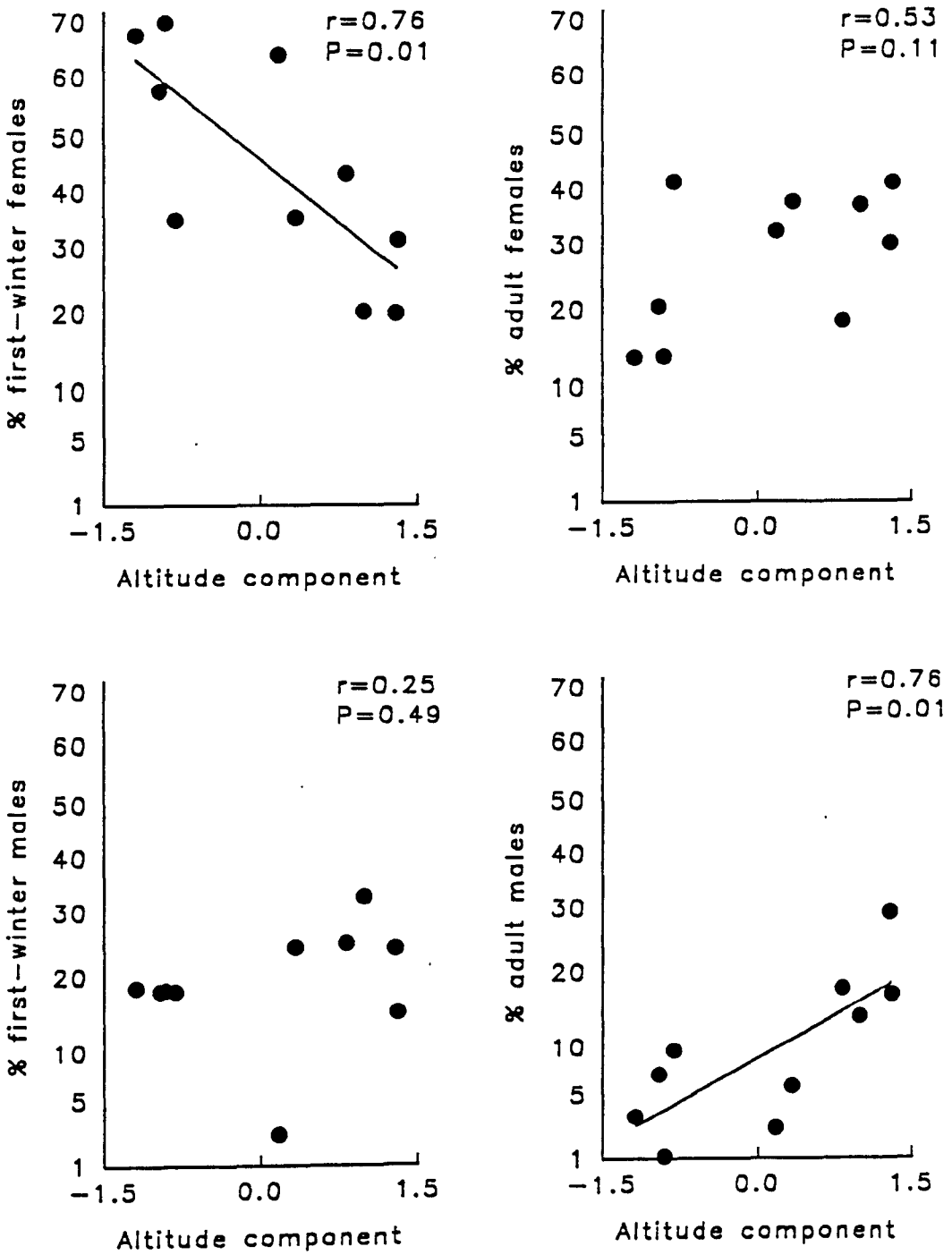


Fig.4.2. Percentage of each age/sex category among Snow Bunting populations in North-east Scotland in Mid Winter (i.e. captures in January and February only), plotted against the principal component Altitude. *Note that the percentage of each age/sex category is presented on an arcsine transformed scale.*

related to relative predation risk. Predator density decreases with altitude, in association with lower prey densities (e.g. Sparrowhawk, Newton *et al.* 1986). This is especially true in winter when there is an exodus from the Scottish uplands of some avian predators known to hunt Snow Buntings, including Merlins (Bibby 1986, Heavisides 1987), Kestrels (Snow 1968, Village 1985), Peregrines (Mearns 1982) and male Hen Harriers (Marquiss 1980). Potential avian predators (Peregrine, Merlin, Kestrel, Sparrowhawk and Hen Harrier) were seen on only 47 occasions during 3284 hours of November to April fieldwork at one high altitude site, Cairn Gorm, during 1987/88 to 1992/93. Although a third of these sightings involved chases of Snow Buntings (one chase per 200 hours of observation, mainly by Sparrowhawks and Merlins), only one Sparrowhawk attack was known to be successful. Sightings of ground predators were also rare on Cairn Gorm (Stoat/Weasel seen only six times despite the tendency of Snow Buntings to mob them), although I did receive one report of a successful Weasel attack on a Snow Bunting. Reduced predation risk may therefore be a major advantage associated with wintering at higher altitudes.

It is also possible that Snow Buntings gain cross-seasonal advantages by wintering at higher altitudes since the habitat and conditions found as altitude increases will become increasingly similar to those they must experience on their Arctic breeding grounds. Individuals which have had more practise in such conditions (by wintering in extreme environments) may be able to risk returning to the breeding grounds earlier, might have higher survival prospects if the breeding grounds are unsuitable on arrival, or be better able to find food in order to deposit egg-laying reserves or feed chicks. In addition, they may be better able to cope physiologically with the range of conditions likely to be encountered on return to the breeding grounds since they are already acclimatised to such conditions (e.g. Barnett 1970, Swanson 1990).

Climatic influences lower the altitudinal zonation of habitat types at higher latitudes. Choice of higher latitude areas outside the breeding season may occur for similar reasons as I have proposed for altitude: reduced competition due to unpredictable food supplies, lack of predators, and familiarity/acclimatisation to breeding habitats. Consequently, if northern sites are mainly occupied by competitively-able adults and males, a degree of latitudinal segregation will result. It is also possible that Snow Buntings do not compete for such habitats, but rather that they assort according to the habitat that provides those environmental conditions best suited to their individual physiological requirements. On this basis most young and female Snow Buntings may be better suited to the less severe climate of lower latitudes and elevations because they have less experience and are smaller respectively.

In conclusion, explanations of site choice by wintering birds that are based solely on the costs of migration distance may not be adequate if climatic- or habitat-related factors, as outlined above, are not taken into account. If possible, future studies of differential migration should concentrate on age and sex composition patterns within habitat types, or attempt to show that the distribution of preferred habitat types is not correlated with latitude.

Chapter 5: POPULATION SIZE, COMPOSITION AND MOVEMENT PATTERNS AT HIGH ALTITUDE SITES

5.1 INTRODUCTION

To maximise overwinter survival, an individual must continuously assess the relative fitness costs and benefits of remaining at its present site or moving to another. These decisions will be influenced by factors specific to the site (e.g. food availability or predictability, predation risk, intra- or inter-specific competition, energetic costs of moving to a new site) and to each individual (particularly age, sex, body-size, energy reserves, competitive ability, foraging ability and prior site experience).

Much of our understanding of the intricacies of these decisions comes from field and laboratory studies of flocking passerines. Most studies have focussed on species exhibiting high site tenacity and well-developed peck-orders (e.g. Dark-eyed Junco, Ketterson & Nolan 1976, Ketterson 1979a; White-throated Sparrow, Schneider 1984; White-crowned Sparrow, King *et al.* 1965; Willow and Crested Tits, Ekman 1979). In such species food availability may limit the number of individuals able to overwinter successfully, either through exhaustion of a finite food resource (Pulliam & Enders 1971), or depletion to levels unable to support all the birds at times of increased energy demands (Schneider 1984). To avoid such over-exploitation, flocks may maintain exclusive territories with limited flock membership, stabilised through dominance hierarchies and high levels of aggression shown to intruders (e.g. Smith 1976, Balph 1979). Subordinate individuals unable to join, or forced out of, these flocks from aggression or limited feeding opportunities may suffer higher mortality in marginal habitats (Fretwell 1969, Ekman *et al.* 1981). Alternatively, they can attempt to join other flocks, but may again suffer because prior occupancy may outweigh competitive ability in deciding rank of incomers, and high levels of aggression shown to incomers may increase stress (Yasukawa & Bick 1983, Schwabl *et al.* 1988). Under such circumstances, changes of wintering site are costly and hence infrequent: a last gasp measure.

Information on species showing greater plasticity in winter site choice is less complete, perhaps due to the difficulties involved in relocating individuals. Greater mobility may be related to temporal instability of food supplies (e.g. Jenni & Jenni-Eiermann 1987, Beckoff & Scott 1989) or the benefits of remaining in flocks (for review see Barnard & Thompson 1985). Senar *et al.* (1992a) described how some individuals amongst a population of Siskins, small tree-feeding finches normally thought to be nomadic (Newton 1972), became resident at a plentiful and stable food supply. Variation in quality of sites, and variation amongst individuals in their ability to realise a site's potential (perhaps as a result of differences in body-size, agonistic ability or experience), may still cause a non-random dispersion of mobile populations between habitats or areas (Caraco 1979, Caraco *et al.* 1989, Peach & Fowler 1989).

Chapter 4 argued that age and sex influenced Snow Bunting settlement patterns in North-east Scotland,

with older birds and males being more likely than their counterparts to be found at higher altitudes. It did not, however, detail the extent to which population composition changed within or between winters. Populations of highly mobile or nomadic species could show rapid changes in numbers and age/sex composition. The first aim of this chapter is to describe the extent of population variation at the upland sites over the entire six-winter period, taking into account methodological difficulties associated with assessing population composition from trapped birds alone. Next, I look at the effects of altitude on Snow Bunting site choice *within* one high altitude site, and the impact that snow can have on both foraging altitude and population composition. Finally, to demonstrate the mobility of Snow Buntings visiting the Cairngorms, I present a summary of the recorded movements of marked birds to, from and between my study sites.

5.2 METHODS

Regular catches of Snow Buntings were continued at Cairn Gorm, Glen Shee and The Lecht (the three highest altitude sites at which birds were trapped for the analysis described in the previous chapter) during winters 1989/90 to 1992/93. The main purpose of these catches was to colour-ring unmarked individuals and therefore catches were preferentially taken when the proportion of unmarked (less experienced) individuals was high. The catches may have been further biassed towards inexperienced birds if birds which had been caught previously were more likely to avoid the trapping sites.

Population size (and composition after November 1989) were assessed from field observations of Snow Buntings on Cairn Gorm, the main study site. I visited Cairn Gorm on at least 100 days during November to April in each study winter, apart from the pilot winter of 1987/88 when a wider selection of sites were visited over a shorter period. Visits to Cairn Gorm were most frequent during the main winter period from December to February (73% of all such days, excluding 1987/88; **Table 5.1**). Visits were less frequent during snow-free periods when birds were less easily seen (see later). There were also several days each winter when Cairn Gorm was stormbound: deep drifting snow usually prevented or delayed access to the study site on these occasions.

Within Cairn Gorm, I mainly visited baited areas or other sites where I anticipated that birds would be found (see **5.3.4**). However, visits were also made to other sites when time allowed, or if birds were not found in the expected places. Although not systematic, these give some indication of the pattern of site use.

Table 5.1. The number of visits each month to the Cairn Gorm study area during winters 1987/88 to 1992/93.

	Number of visits (days) in:						
Year	November	December	January	February	March	April	Total
1987/88	0	1	13	7	13	3	37
1988/89	17	16	17	24	23	21	118
1989/90	13	24	26	23	25	13	124
1990/91	12	25	24	24	18	11	114
1991/92	15	23	23	23	26	13	123
1992/93	17	21	26	12	15	9	100

Each day, on each visited Level, I recorded the length of time I was present and the minimum number of birds seen. When birds were seen well, I estimated the percentage that were ringed and noted the identities of as many colour-ringed birds as possible. I also recorded the age/sex categories of unringed birds (see **3.3.5** and **6.2**). On days where several flocks were seen and flock composition changed, scans were made more frequently and the overall age/sex composition of unringed birds was estimated from the sum of sightings of unringed birds of each age/sex category in relation to all sightings of age/sexed unringed birds. At the end of each day I attempted to compile a register of the birds seen. This comprised:

i) an estimate of the number of birds seen and the time I spent on each level; and

ii) an estimate of the number of birds seen on the *whole* Ski Area (Levels 1-3 combined), the percentage ringed, and the approximate age/sex composition of birds seen (calculated from the identities of colour-ringed birds and unringed birds, and their relative frequency). Individually ringed birds were often seen at more than one level on the same day, so the estimated number present on the Ski Area could not be calculated simply from the sum of birds seen on each of Levels 1-3. Instead, the identities of individuals seen on each level had to be taken into account. The percentage of birds ringed was only recorded if a large proportion of birds were seen well. Similarly, I discarded estimates of the relative frequencies of each age/sex category if I was unable to record either a) the identity of less than 80% of ringed birds estimated to be present in the flocks seen, or b) the age/sex category of less than 80% of the estimated number of unringed birds present.

To help explain changes in the number and composition of birds present on Cairn Gorm, I also describe the pattern of movements noted between sites in North-east Scotland. These mainly result from my own

observations or re-trappings of colour-ringed birds, but some involve birds caught by bird-ringers elsewhere.

5.3 RESULTS

5.3.1 Age/sex composition of catches

Although there was variation between years in the age/sex composition of catches (**Table 5.2**), there was no consistent increase or decrease in the relative proportions of any of the age/sex categories over the six winters from 1987/88 to 1992/93 (**Figs.5.1 & 5.2**). I used chi-square tests within site and winter period categories to compare the annual proportions of each age/sex category trapped. Where there were significant differences within period and site combinations, these confirmed the impression given by **Fig.5.2**: adults of both sexes were significantly commoner (in relation to the other age/sex categories) in 1990/91, and adult females especially in 1989/90; juvenile females were significantly commoner at the high altitude sites in 1991/92 and 1992/93. These tests, as well as **Fig.5.2**, indicated that the years used to analyse differences in age/sex proportions between sites of different altitude (1987/88 and 1988/89, see **4.2**) were not particularly unusual: juvenile males were slightly commoner than expected in both years and adult females less common in 1988/89.

Did the relative frequency of the age/sex categories vary concurrently? Perhaps juveniles males and females would both be particularly common, for example, after summers of good breeding success. Conversely, adult males and juvenile males might increase and decrease in parallel if site choice was influenced to a variable degree each year by such male characteristics as large body-size or being dominant (**3.3.3, 7.3.3a & 8.3.1**). Therefore, I looked for correlations between the age/sex categories in their relative annual abundance, using the mean annual deviation in the percentage of each age/sex category from their expected percentage frequencies (**Fig.5.2**). Of course, these variables are not entirely independent of each other: if the annual deviation of one age/sex category is unusually high, the mean deviation of the other age/sex categories will automatically be lower. This will artificially increase the significance (i.e. lower the value of P) of results with negative correlations, and decrease the significance of results with positive correlations. It should still, however, give some indication of which age/sex categories were varying in parallel or in opposition to each other. The results of the analysis are shown in **Table 5.3**. In years when adult females were relatively abundant, juveniles, especially juvenile females, were scarce. There was also a slight suggestion that juvenile females were more abundant in years when juvenile males were abundant. Thus age-related explanations for differences in relative annual abundance would appear to be more plausible than arguments based on concurrent increases or decreases amongst the sex categories.

Table 5.2. The age/sex composition of Snow Bunting catches (excluding a small number of birds which could not be aged and/or sexed) at each of the three upland sites in each winter period. *Figures given for each age/sex category are the percentage that each age/sex category formed of the total catch (all years combined) and the range of annual percentages (brackets). The total is the number of aged and sexed birds caught, and, in brackets, the number of winters when there were at least 20 captures.*

Site	Period	Juvenile female	Adult female	Juvenile male	Adult male	Total
Cairn Gorm	Early Winter	20%	37%	19%	24%	338
		(13-28)	(17-49)	(8-30)	(17-41)	(5)
	Mid Winter	16%	39%	19%	26%	483
		(5-31)	(29-48)	(12-23)	(16-36)	(5)
	Spring	42%	29%	18%	11%	531
		(24-71)	(9-45)	(15-29)	(9-21)	(6)
Glen Shee	Early Winter	19%	55%	11%	15%	179
		(10-23)	(40-66)	(7-30)	(7-20)	(3)
	Mid Winter	27%	41%	15%	16%	243
		(22-32)	(32-53)	(11-19)	(8-21)	(5)
	Spring	41%	32%	15%	12%	211
		(29-53)	(23-53)	(7-25)	(8-13)	(4)
The Lecht	Early Winter	29%	40%	12%	20%	199
		(14-65)	(17-64)	(5-19)	(10-30)	(4)
	Mid Winter	22%	38%	17%	22%	157
		(9-30)	(15-48)	(4-32)	(13-52)	(4)
	Spring	56%	21%	19%	4%	135
		(52-59)	(13-23)	(14-33)	(2-4)	(2)

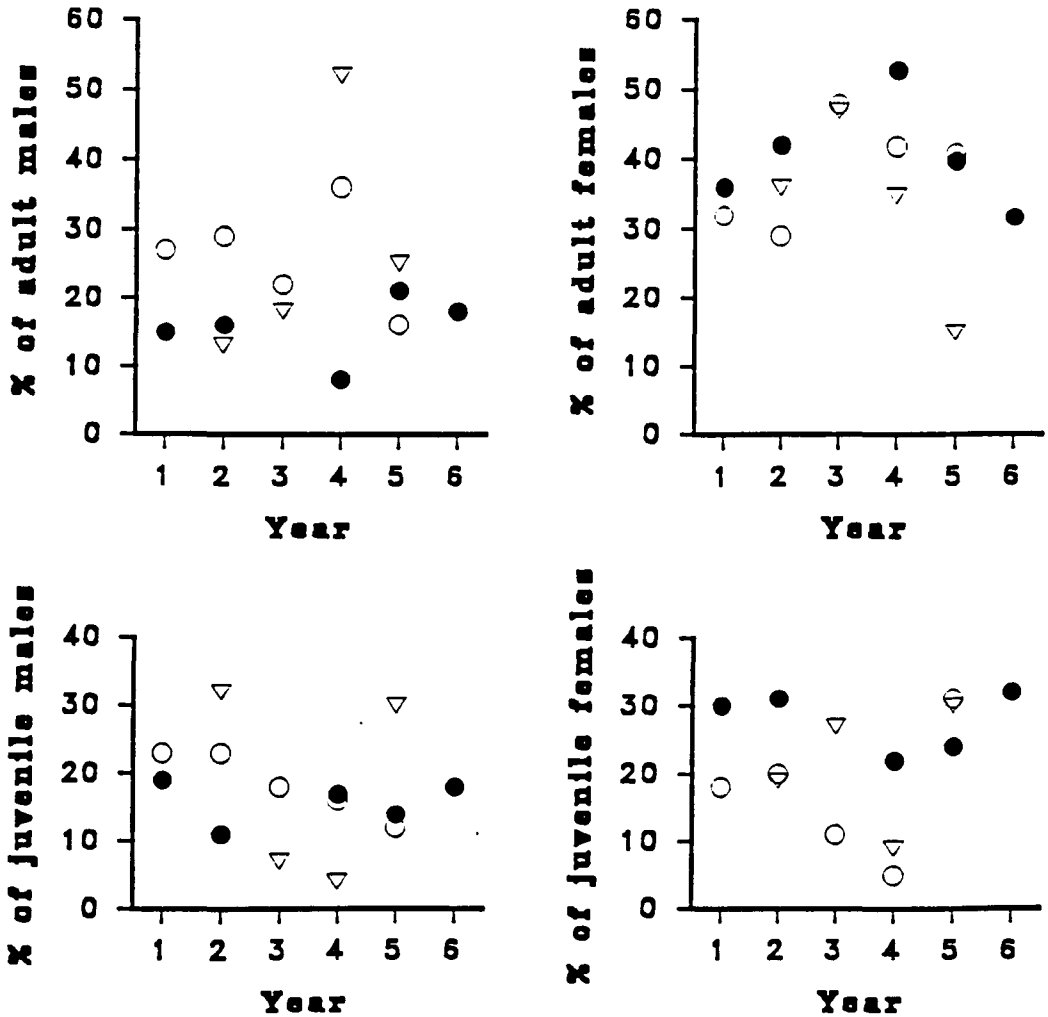


Fig.5.1. The age/sex composition of Snow Bunting catches made at Cairn Gorm (open circles), Glen Shee (filled circles) and The Lecht (triangles) during January and February of the six winters 1987/88 (labelled 1) to 1992/93 (6). *Individuals were only included once each winter. Sites and years where less than twenty birds were caught are not shown. Sample size of birds caught are Cairn Gorm: 98 in 1987/88 (year 1), 111/y2, 147/y3, 78/y4 & 49/y5; Glen Shee: 47/y1, 88/y2, 36/y4, 42/y5 & 22/y6; The Lecht: 47/y2, 67/y3, 23/y4 & 20/y5.*

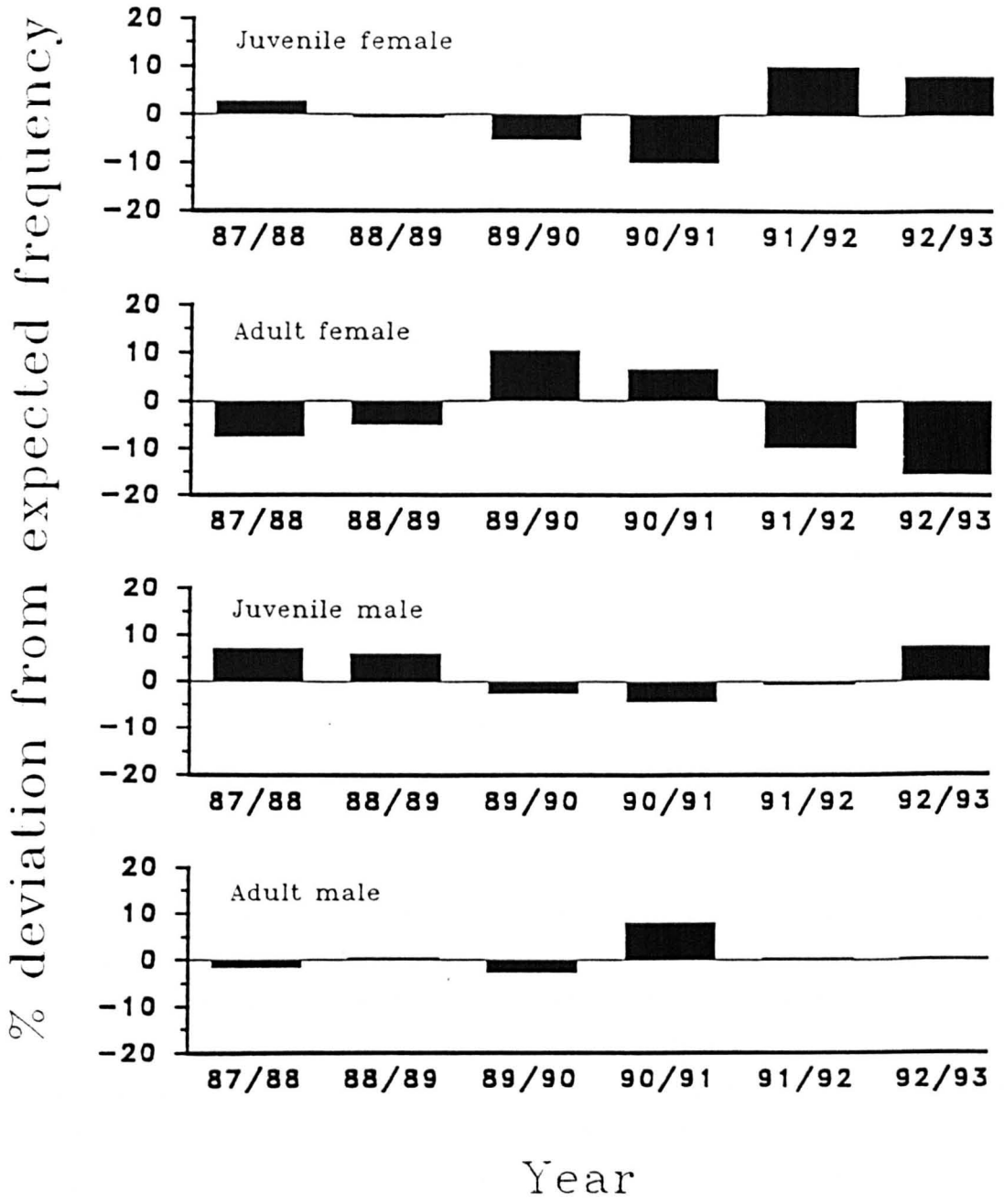


Fig.5.2. Annual variation in the percentage of each age/sex category of Snow Buntings trapped at the three high altitude sites. *Figures, derived for illustrative purposes, are the mean annual deviations of each age/sex category from their expected percentage frequencies for a given site and winter period. The expected percentage frequency of an age/sex category for a given site (Cairn Gorm, Glen Shee or The Lecht) in a given period (Early Winter, Mid Winter or Spring) was the percentage that the age/sex category formed of the whole sample of aged and sexed Snow Buntings caught at that site in that period over all six winters combined (**Table 5.2**). I then subtracted this expected percentage frequency from the annual percentage that an age/sex category formed of the catch for each site and period (omitting percentages based on a sample of less than twenty birds), producing an annual deviation for each site/period, from which a mean was taken for each year.*

Table 5.3. Spearman Rank correlations between pairs of age/sex categories of Snow Buntings in their annual deviations from their expected percentage frequencies (definition and derivation given in legend to Fig.5.2**).** *Positive correlations indicate that the relative annual abundances of the pair of age/sex categories increased or decreased in parallel, while negative correlations indicate that one age/sex category increased in years when the other decreased. In all cases, six pairs of annual deviations were compared. Significance (P) is given in brackets, but see caveats in text.*

	Adult female	Juvenile male	Adult male
Juvenile female	-0.89 (0.018)	0.66 (0.16)	0.03 (0.96)
Adult female		-0.77 (0.07)	-0.37 (0.47)
Juvenile male			-0.09 (0.87)

5.3.2 Trapping bias

The analyses presented in **4.3** and **5.3.1** describe the age/sex composition of samples of trapped birds, but it is possible that some age/sex categories were more likely to be trapped than others. Hence age/sex composition of trapped birds may not have truly reflected the age/sex composition of Snow Buntings present at a site. This section investigates the role of perhaps the most influential determinant of whether or not a bird which was present got caught, namely site experience. Experience could act in two ways. Firstly, it could *increase* an individual's probability of being captured at a baited area if experienced birds were more likely to find the baited area and sufficient food was provided to offset the risks of being trapped. Alternatively, experienced birds may be caught less frequently if they recognise times and places when the risk of capture is high, and therefore avoid them. To investigate such possibilities, in this section I compare the recapture rates of marked birds in relation to a measure of their experience, i.e the number of times they had been seen at Cairn Gorm subsequent to their first capture.

During winter 1989/90, I calculated the percentage of birds which I recaptured on the first, second, third .....nth day on which they were observed after their initial capture (*not* the interval between capture and resighting because some individuals may have used Cairn Gorm more frequently than others, hence building up site experience more rapidly). No effort was made to target previously ringed birds in catches - they were recaptured incidentally as part of larger catches of unringed birds. To a small extent, I *avoided* capturing ringed birds (i.e. I was more likely to decide to take a catch if the ratio of unringed:ringed birds

was high, see also **2.5**). However, the results should not be affected because I did not consciously avoid capturing *particular* ringed birds or experience categories. In essence, I found that the more often an individual had been seen since its initial capture, the less likely it was to be retrapped (**Fig.5.3**; chi-square test for differences in retrap rates between birds being seen on the 1st, 2nd, 3rd-4th, 5th-6th, 7th-10th, 11th-20th and 21st-50th times: $X^2_6=23.2$, $P<0.001$). Also, as expected, birds which had returned to the study area, having been present in previous winters, also had lower recapture rates (**Fig.5.3**). It therefore seemed that as birds spent more time on the study area, they became trapshy (i.e. increasingly difficult to trap). Hence estimates of the population composition of Snow Buntings at sites, if based on trapped samples, may be biased towards inexperienced (often young) birds.

5.3.3 Age/sex composition of catches versus sightings

If age or gender affected the length of time that a Snow Bunting spent at a site, or its likelihood of being trapped, then trapshy behaviour could result in inaccurate estimates of the age/sex composition of Snow Buntings at a site, if these were based on samples of captured birds. Therefore I made field observations of the age and sex of Snow Buntings at Cairn Gorm on a near-daily basis during winters 1989/90 to 1992/93 (**Table 5.1**) in order to compare the age/sex composition of catches with the actual age/sex composition of birds present.

I summed the number of sightings of each of the four age/sex categories on each day that an acceptable estimate of age/sex composition was made (see **5.2**), aggregating the data into the three winter periods and removing sightings of known Scottish breeding birds (as in **4.3** and **5.3.1**). I then compared the percentages of each age/sex category trapped with the percentage sighted in each period, using Wilcoxon matched pairs tests. Data for each winter were kept separate, generating a maximum of twelve cases (4 winters x 3 periods) for each test. In practise, there were 11 cases for each test because no birds were trapped in Mid Winter 1992/93. On average, there were 14% more adult males in the sighted samples than the trapped samples ($z=2.93$, $P=0.003$). This was compensated by a 12% reduction in sighted juvenile females compared to trappings ($z=2.80$, $P=0.005$), and a tendency also for juvenile males to be less frequently seen than trapped (3% reduction, $z=1.72$, $P=0.09$). In conclusion, it appeared that estimates of age and sex composition based only on trapped birds underestimated the relative abundance of male and adult Snow Buntings on Cairn Gorm.

Therefore the next two sections of this chapter use age/sex composition estimates based on the daily estimates from field observations. Further analyses also include the minority of birds which were known to be of Scottish breeding origin, but ignore data from Spring when winter resident birds fatten and leave the site, and migrants were known to pass through (see **5.3.6** and **8.3.12a**).

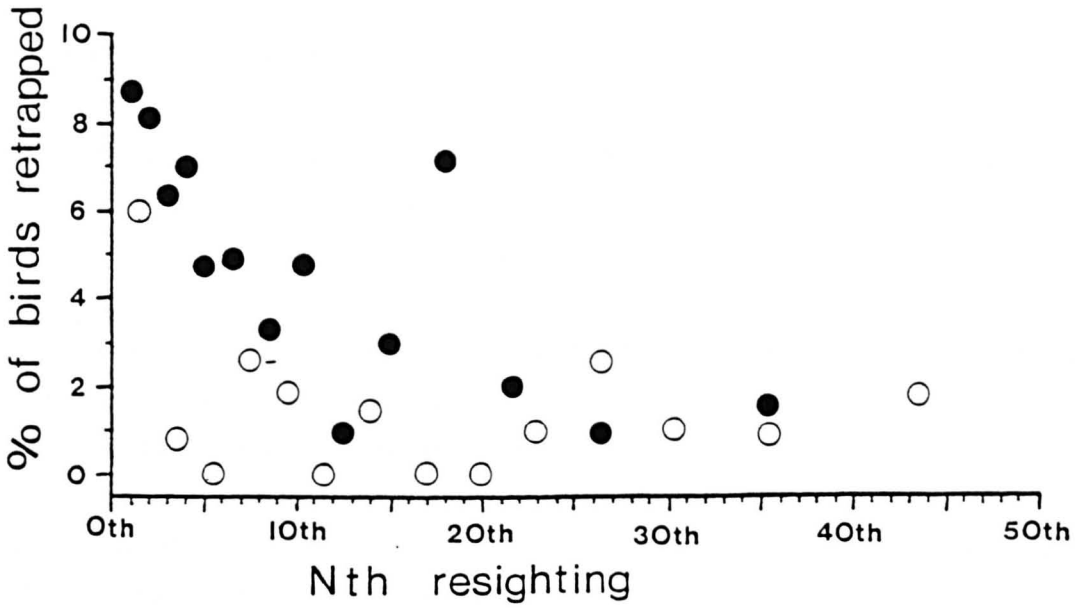


Fig.5.3. The daily recapture rate of Snow Buntings in relation to the number of times (days) they had been resighted at Cairn Gorm in 1989/90. *The circles represent the percentage of birds that were retrapped on the nth day that they were* seen *in 1989/90. Filled circles depict data from birds which were* first *caught in 1989/90, hollow circles data from birds which returned having been caught in a previous winter. Sightings were aggregated into groups of days to ensure that each circle depicted at least 100 sightings, e.g. the furthest right circle represents 2 captures of individuals seen on 110 occasions for the 39th-56th (average=44th) time in 1989/90 (including up to 18 resightings of the same individual on different days).*

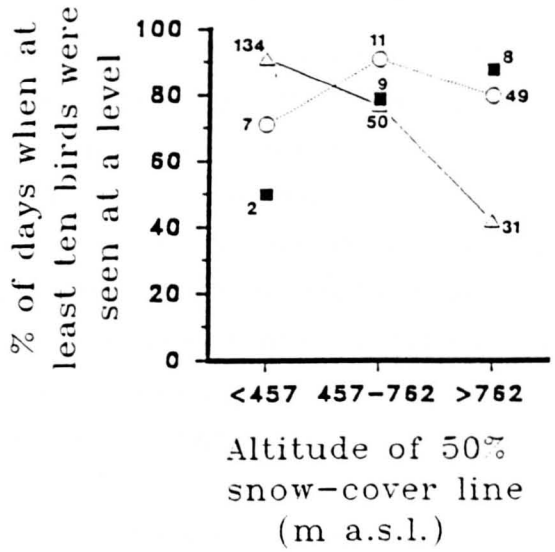


Fig.5.4. The percentage of observation days at each of three altitude levels on Cairn Gorm on which at least ten Snow Buntings were seen, in relation to the altitude above which there was at least 50% snow-cover. *Only days when at least an hour was spent on the level were included. Sample sizes (number of observation days) are included on the figure. Level 1 (triangles) lies between 500m and 650m, Level 3 (circles) between 850m and 1100m, and Level 4 (squares) between 1000m and 1309m a.s.l. Snow Buntings were less likely to be seen on Level 1 on days when the 50% snow-cover line was above 762m.*

5.3.4 Numbers on Cairn Gorm

Counting Snow Buntings on Cairn Gorm was not easy because of the species' highly mobile nature, the large study area, and the rugged, mountainous nature of the terrain. Counts above the car parks (above Level 1) were time consuming and were not made on a regular basis.

In order to examine the effect of snow on Snow Bunting distributions *within* Cairn Gorm, I selected counts from a given level (Levels 1, 3 or 4) which lasted at least an hour. Counts were only made during 1989/90 to 1992/93, and between December to February (because earlier and later data may have been affected by lack of site knowledge of newly arrived early winter birds or spring migrants). I then determined the percentage of days on which at least 10 Snow Buntings were seen on a given level in relation to the altitude of the 50% snow-cover line (see **2.3**). The probability of seeing at least ten birds increased on Level 1 as the 50% snow-cover line descended (**Fig.5.4**, $X^2_2=39.7$, $P<0.001$). The sample size of visits to the other levels was too small for a meaningful analysis. However, the likelihood of seeing ten or more Snow Buntings on Level 3 peaked when the 50% snow-cover line was between 457m and 762m, and on the highest ground (Level 4) when the 50% snow-cover line was above 762m. Despite the availability of bait on Level 1 at all times, I was significantly more likely to encounter ten or more Snow Buntings on Level 3 than Level 1 when the 50% snow-cover line was above 762m ($X^2_1=10.2$, $P<0.01$). Therefore, when site choice was not limited by snow-cover, Snow Buntings appeared to choose to forage at higher altitudes *even within Cairn Gorm*, and spent less of their time at lower altitudes.

Given this result, the mean of all counts from Level 1 would underestimate the number of Snow Buntings using the Ski Area. Therefore, to estimate population trends there, I calculated both the maximum monthly counts on Level 1, and the median monthly counts on Levels 1-3 combined (**Table 5.4**). The former should be relevant because complete snow-cover was present on Level 1 (thus forcing most birds down to this level) on at least 2 days in every month from November to April during the study period. However, they may be sensitive to some extreme counts. The median counts may therefore depict population trends more accurately, despite being partially based on counts made when only a small proportion of the population was seen. Their accuracy was hopefully improved, however, by only including the visits I made to the Ski Area which lasted at least one hour (except in 1988/89 when visits were not timed and all visits were used).

The maximum counts were relatively stable during four of the five mid-winters with adequate data, but were higher in 1989/90. Median winter counts, however, were higher during 1988/89 to 1990/91, then dropped in both the next two winters. In association with this, many more birds were trapped during 1988/89 to 1990/91 than were ever seen at one time (**Table 5.4**), indicating some degree of turnover of birds in these years. Thereafter, despite no reduction in trapping effort, fewer individuals were trapped and the marked population appeared more stable.

Table 5.4. Maximum and median monthly counts of Snow Buntings on Cairn Gorm, and the annual number of birds handled during the winter period (excludes March and April trappings which probably included individuals which were on migration - see 5.3.6 & 8.3.12a). *The maximum count only used data from Level 1, the median count used data from Levels 1-3 combined (see text). Counts for winter 1987/88 are not presented because individual birds could not be distinguished (therefore preventing discrimination between flocks seen on the same day).*

	Maximum/median monthly counts in:						No. of individuals trapped
Year	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Nov. to Feb.
1988/89	30/45	40/30	80/45	80/60	125/85	40/18	183
1989/90	150/80	120/75	90/58	130/40	110/40	80/41	276
1990/91	50/42	60/40	70/40	85/65	75/19	32/17	120
1991/92	50/20	70/31	75/40	70/45	75/22	29/11	74
1992/93	80/ 4	60/24	75/29	70/10	50/25	75/42	40

5.3.5. Population composition in relation to snowfalls

Maximum counts of Snow Buntings on Cairn Gorm were markedly higher than median counts throughout each winter (**Table 5.4**), suggesting a continuous state of population flux. We can surmise that different sets of individuals contributed to the population maxima, because of the large overall number of birds trapped in some winters (**Table 5.4**). A considerable part of the Snow Bunting population using Cairn Gorm at any one time must therefore have been prone to move between sites, as hypothesized in **1.2**. The aim of the present section is therefore to investigate whether or not the proposed causes of population movements, namely alternating periods of snow-cover and thaw (**1.2**), were associated with changes in Snow Bunting numbers and population composition on Cairn Gorm.

Snow Buntings have been noted feeding on scraps dropped by skiers ever since the first mechanised downhill ski areas were developed in Scotland (Hillcoat 1962, Watson 1977). I attracted them to bait (with the aid of a tape lure) within an hour of my first visit to Cairn Gorm in January 1988. Not surprisingly, therefore, they rapidly came to my regularly baited spots (usually CIFS, CCPB or CIB, see **Fig.2.1**) when forced down to lower levels by snowfalls (**5.3.4**). The percentage of birds which were colour-ringed, and

the age/sex composition of flocks attracted to the baited areas could usually be easily ascertained at these times.

However, before snowfalls, when Snow Buntings generally fed at higher altitudes, they were less easily found, less approachable (observations were usually made from a parked car on Level 1) and more mobile. Estimating age and sex composition was more difficult, except when birds visited the less frequently baited CCTB and PTB (**Fig.2.1**). Often, especially if the higher ground was largely snow-free, Snow Buntings visited the high-altitude bait patches infrequently, presumably because feeding elsewhere was more profitable or less risky. Also, because these high altitude bait patches were not provided regularly, the birds finding them first could have been those with previous site experience. To prevent these more experienced individuals from perhaps biassing estimates of the age/sex composition of the Cairn Gorm Snow Bunting population prior to snowfalls, in the following analysis I have only included snowfalls where the mean number of birds seen before the snowfall was *higher* than that after the snowfall.

I selected the five days before a snowfall (snow down to at least 670m, as defined in **2.4**), or less if some of these days had snow-cover from a previous snowfall. Then, for days where data were available, I calculated the mean percentage of birds on the Ski Area (Levels 1-3) which bore colour-rings and the mean percentage of each age/sex category in the population. These were compared with the same parameters for the five days (or less if the ground became snow-free) following (and including) the first day of a snowfall.

For those six snowfalls in which more birds were seen before than after a snowfall, the mean percentage of colour-ringed birds *increased* following the snowfall (Wilcoxon matched pairs test: $z=1.99$, $P=0.046$). In association with this, the percentage of males, particularly adult males, also increased (Wilcoxon matched pairs test for adult males: $z=2.20$, $P=0.028$). I interpret this as a movement of Snow Buntings away from the montane areas during winter snowfalls, especially of females and birds with little previous site experience. Consequently, there was an increase in the proportion of males and experienced birds amongst those able (or choosing) to remain. A well documented example of this, and the subsequent return of birds following the end of the snowfall, is illustrated in **Fig.5.5**.

I then looked for a relationship between the *quantity* of snow and the subsequent age/sex composition of birds remaining at Cairn Gorm. All snowfalls could now be included, because only data on the age/sex composition post-snowfall was required. However, was it best to use an average from the daily age/sex composition estimates, or some other measure? Snow rarely fell in one short heavy burst, but often accumulated over several days. I noticed that in some snowfalls larger numbers of birds were seen in the early part of the first day of a snowfall than thereafter, possibly because emigrants had not yet decided to leave. I therefore excluded data from the first day of a snowfall. Likewise, it was not uncommon for snow-cover to last for several weeks (still by definition the same snowfall, **2.4**), allowing some emigrants to return when better, more stable conditions prevailed (e.g. anticyclones). To prevent this from affecting my

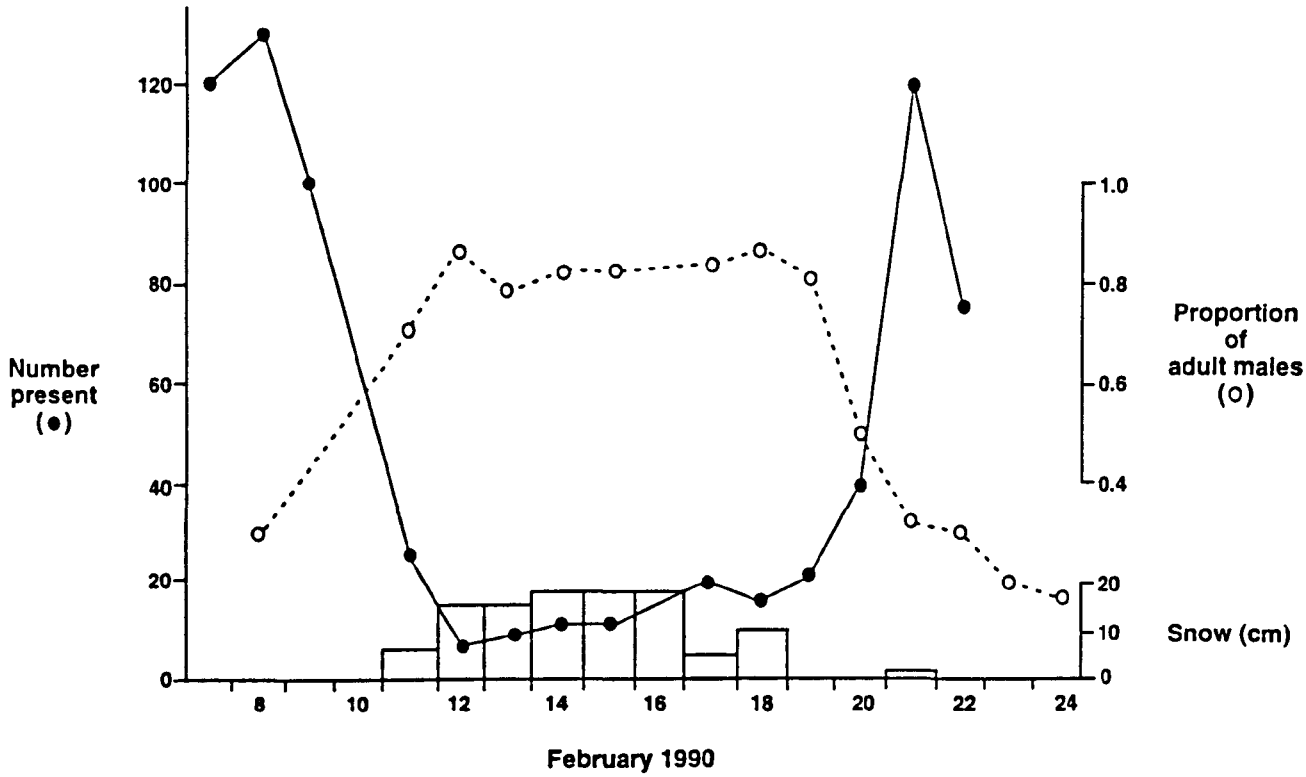


Fig.5.5. An example of the short-term changes in the number of Snow Buntings seen on the Cairn Gorm Ski Area and the proportion of these that were adult males, associated with a snowfall.

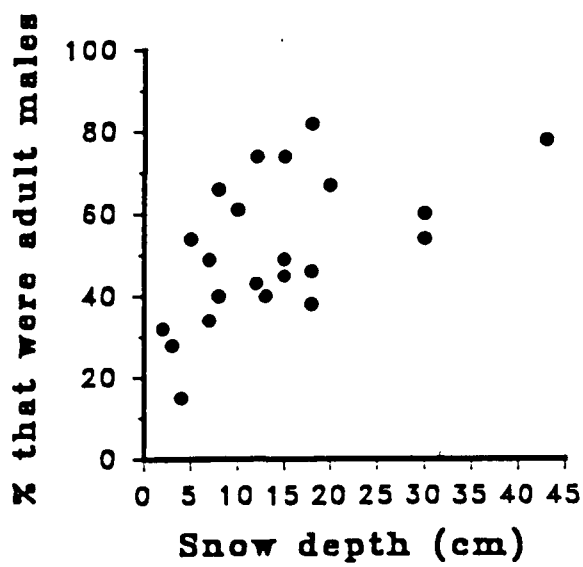


Fig.5.6. The relationship between snow depth and the percentage of Snow Buntings remaining at Cairn Gorm following a snowfall which were adult males. *The percentage of adult males was calculated on the day with the maximum count of birds during the 2nd-5th day after the first day of the snowfall. The snow depth was the maximum experienced up to the day when the maximum count occurred. The percentage of adult males increased with snow depth (Table 5.5).*

results, I only considered data from the 2nd-5th days of a given snowfall for analysis. I then selected the day with the *maximum* count of Snow Buntings, and calculated age/sex composition. Use of the maximum was preferred, even though minimums may have better reflected the overall impact of the snowfall, because larger sample sizes should reduce the standard error associated with estimates of percentages. As the number and composition of birds on this day was the product of up to four days of lying snow, I considered that the appropriate weather variable for analysis was the maximum snow depth recorded in the snowfall up to and including the day of the maximum count.

The percentage of adult males increased with increasing snow depth and with decreasing remaining population size (**Table 5.5, Figs.5.6 & 5.7**). Because the number of birds remaining after the snowfall was not related to snow depth (r_s=-0.14, n=22, P=0.27), these results appear to be independent. In association with this, the percentage of females of both age categories dropped when numbers dropped or snow depth increased, but the percentage of juvenile males remained constant (**Table 5.5**).

Table 5.5. Spearman Rank correlations between the percentage of each age/sex category of Snow Buntings remaining following a snowfall and (a) snow depth, and (b) number of birds remaining. *n=22 snowfalls.*

	(a) Snow depth		(b) Number of birds remaining	
Age/sex category:	r_s	P	r_s	P
Juvenile female	-0.41	0.055	0.46	0.033
Adult female	-0.60	0.003	0.47	0.027
Juvenile male	-0.00	0.98	-0.04	0.85
Adult male	0.57	0.006	-0.54	0.010

5.3.6. Movements of ringed birds

The increase in Snow Bunting numbers at Cairn Gorm after snow had melted (e.g. **Fig.5.5**) suggests that the previous reductions in bird numbers were probably largely due to emigration rather than mortality. There have been numerous movements of marked birds between my upland sites, and to and from other

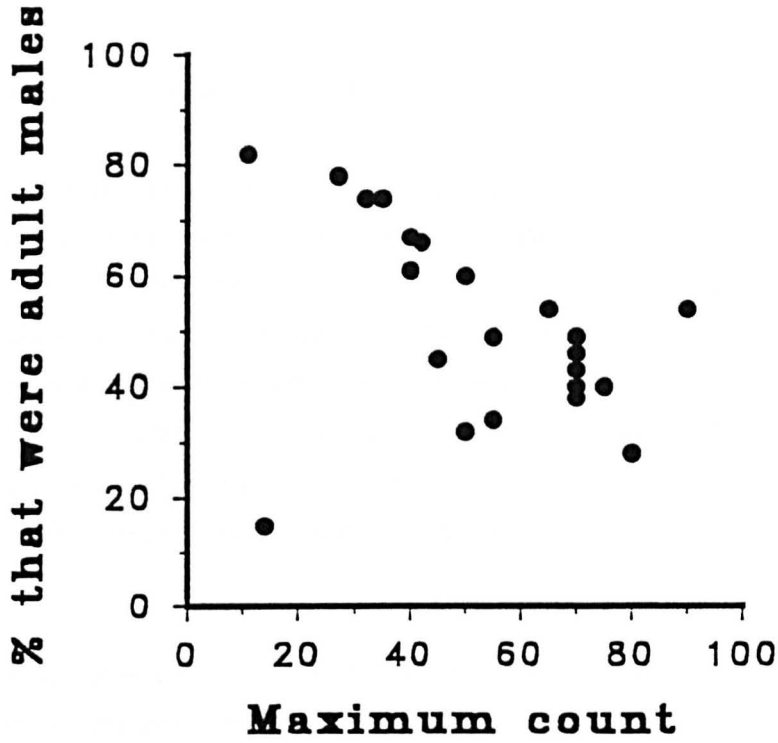


Fig.5.7. The percentage of Snow Buntings remaining at Cairn Gorm which were adult males in relation to the maximum number of birds which were seen there during the 2nd-5th days after a snowfall. *The percentage of adult males was calculated on the same day as the maximum count. The percentage of adult males was higher when the number of birds which remained was low (**Table 5.5**).*

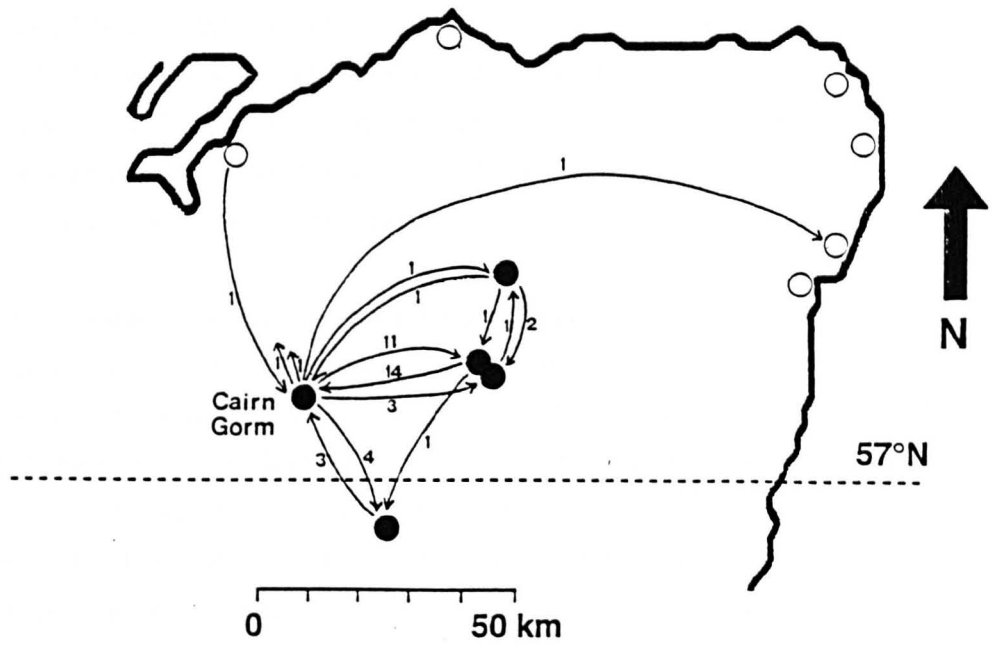


Fig.5.8. Winter movements of Snow Buntings involving upland sites in North-east Scotland. *Only movements occurring within the same November-February period are shown (n=46). Filled circles represent my five trapping sites, open circles other trapping sites operated by local bird-ringers during the study period.*

sites in Britain and abroad, to illustrate this further.

Since 1987/88, a minimum of 180 movements involving my five upland sites have been recorded. This excludes several birds which I failed to catch at my sites which only had metal rings (i.e. marked at unknown sites elsewhere by other bird-ringers). It is also likely that my sightings of site-only marked birds (see **2.5**) represented more movements than I recorded because only the first sighting of a non-unique combination from another site was considered valid, unless birds could be distinguished by their age and sex. The number of movements also excludes a minimum of 23 movements between Corgarff and the Lecht, as these sites are only 4km apart. The 180 movements involved at least 145 individuals, but 23 birds moved more than once (maximum six movements). Three birds were recorded at three sites, and another at four.

In total, 46 (26%) movements occurred within the same November to February period (**Fig.5.8, Table 5.6**). Within-winter movements were relatively short: only two were over 50km, and no birds were known to move outwith North-east Scotland (**Fig.5.8**). It was seldom possible to pinpoint the date of movement to less than a fortnight due to the scarcity of visits to sites other than Cairn Gorm. Hence, it is also possible that some birds may have wandered widely after leaving one site and before arriving at another. A few established Cairn Gorm individuals did, however, have better documented movement schedules. The juvenile male 'GNMY', for example, was one of the birds which moved from Cairn Gorm during the snow spell shown in **Fig.5.5**. It was seen there on 17 dates from late November until 9th February (just before the snowfall), was next noted at The Lecht on 16th February (during the snowfall), but was back at Cairn Gorm on the 21st February (after the snowfall) and frequently thereafter until the end of the winter. The adult female 'OYBM' and the adult male 'LGMB' showed a slightly different pattern, moving to and fro from Cairn Gorm to the Lecht several times during the course of one winter. Many other Snow Buntings, however, were only seen at the sites they visited on single occasions, perhaps indicating that they had more regular sites elsewhere, or were more nomadic.

Altogether, 59 movements were recorded from individuals known to be at one site during the non-breeding season, and *first seen* at another in spring (March or April) of the same non-breeding season (**Table 5.6**). Thirty-six of these again involved movements of up to 70km between inland sites in North-east Scotland. Eleven, however, were of birds which had been seen/trapped earlier that winter or even the same spring at coastal sites in England or Holland and were probably on their northward migration when passing through the Cairngorms. Four birds were subsequently trapped in the same spring in Iceland, the likely destination of the majority of Scottish inland wintering Snow Buntings (Smith in prep.).

Table 5.6. The minimum number of movements of Snow Buntings recorded between sites in the North-east Scottish uplands and elsewhere. *'Same Winter' movements were those where an individual's last definite sighting date (departure date) at one site and first definite sighting date (arrival date) at another site were during the same November-February period. 'Future Winter' movements were those where the departure date was in a previous non-breeding season (November-April) to a November-February arrival date at a new site. 'Same Spring' and 'Future Spring' movements refer to March-April arrival dates for same non-breeding season or previous non-breeding season departure dates respectively. The 'Other' movements are a bird trapped in Iceland in May, and a bird found dead in June on coastal Grampian. Movements between The Lecht and Corgarff were not included because the sites are only 4km apart. Multiple movements of the same individual are included each time they changed site.*

From:	To:	Same Winter	Future Winter	Same Spring	Future Spring	Other
Cairn Gorm	Glen Shee	4	8	1		
	The Lecht	11	7			
	Corgarff	3		4		
Glen Shee	Cairn Gorm	3	3	12	2	
	The Lecht			2		
	Corgarff			1		
The Lecht	Cairn Gorm	14	5	10	1	
	Glen Shee	1	3			
Corgarff	Cairn Gorm		7	1	1	
	Glen Shee			2		
Cairngorms a	Upland NE Scotland b	4	1	1	1	
	Coastal NE Scotland c	1		3		1
	Coastal UK d		4	1	2	
	Holland		3			
	Iceland		2 e	4	3	1
Upland NE Scotland	Cairngorms	4	2	2		
Coastal NE Scotland		1	6	4		
Coastal UK			2	10	2	
Holland				1		
Iceland			8 f			
Σ		46	61	59	12	2

a Cairn Gorm, Glen Shee, The Lecht & Corgarff

b The Cabrach, Cairn o' Mount & Aviemore (see Fig.2.2)

c Ardersier (Highland), Newburgh, Balmedie & Rattray (all Grampian)

d Musselburgh (Lothian), Seaton Carew (Cleveland), Filey (Yorkshire), Titchwell (Norfolk), Kessingland (Suffolk), Shoeburyness (Essex), Sandwich (Kent), Anglesey, Lundy.

e Includes one bird found dead on a North Sea oilrig (58°N) in November.

f Includes one bird from the Faeroes

There were 73 movements with one or more intervening breeding seasons between the last sighting at one site and the first at another. Eight of these were from birds first trapped at possible breeding locations in Iceland and The Faeroes, then recaught in winter in the Cairngorms. Nine resightings of birds first trapped in the Cairngorms were on southern UK coasts or Holland. Only six of these involved individually marked birds, but all had been first recorded in the Cairngorms from 28th February to 25th March, presumably when stopping off there on their northward spring migration. Their recovery dates, mostly in November to February, perhaps imply that the southern recovery sites were their wintering areas.

Two birds spent long periods (at least a month) at one high altitude site in North-east Scotland in one non-breeding season and then returned in the next to spend at least a month at a *different* high altitude site. They were not seen at their original sites in the second winters, suggesting that they had opted for new wintering localities on their return, although remaining in the same general wintering area. There were also nine inter-site movements between winters which suggested that some birds may have chosen higher altitude or higher latitude sites in subsequent winters. Interestingly, all nine were juvenile females when last seen at their low or southerly sites, although this age/sex category does predominate at such sites (see **4.3.3**). Four were seen on numerous winter occasions after arrival in the Cairngorms, indicating that they had settled at or near their new location. Another moved from Scotland to Iceland between winters, and its sighting date in Iceland (21st January) suggested that it had been there all winter.

Altogether, 39% of the 74 movements to Cairn Gorm (excluding two Scottish breeding birds) involved individuals which were seen on only one day (they may have been present longer, but are unlikely to have been visiting the lower levels on Cairn Gorm during snow for longer). Seventeen (23%) others were seen over a 2-3 day period, 18 (24%) for up to 30 days, and 10 (14%) for more than a month in the non-breeding season in which they arrived.

5.4 DISCUSSION

5.4.1 Annual fluctuations in population size and composition

On Cairn Gorm, both the number of birds at any one time (as judged by the median monthly counts) and their turnover decreased during the latter years of the study (**Table 5.4**). However, maximum monthly counts remained fairly stable during the five winters with adequate data (counts c60% higher in 1989/90, the year with the maximum turnover), perhaps suggesting some sort of ceiling to the population size on Cairn Gorm. Age/sex compositions did not show great fluctuations between years - the maximum deviation from the expected percentage of birds trapped of any age/sex category in any of the six winters was 16% (adult females in 1992/93; **Fig.5.2**). Therefore, despite their capacity for mobility (see **5.3.6**) and differences in turnover rates (**Table 5.4**), Snow Bunting population composition at the high altitude sites did not vary greatly between years. Site or area fidelity may have played some part in this (see **5.3.6** and

9.3.4). However, the ability of at least some birds to change wintering areas by hundreds, or even thousands of kilometres (e.g. Scotland to Iceland, **5.3.6**; see also examples in Williamson 1966 and Banks *et al.* 1991b), suggests that a proportion of the population could react swiftly to fluctuating food availability, environmental conditions or population pressure.

Age/sex composition estimates based only on data from trappings underestimated the abundance of adult males on Cairn Gorm by 10-15% (**5.3.3**). Adult males may have had more site experience, because they were the most likely age/sex category to remain on Cairn Gorm during snowfalls (**5.3.5**), and hence under-estimation of their abundance may have been due to trapshy behaviour (**Fig.5.3**). This was matched by an overestimation of the abundance of juveniles, particularly females. In contrast to this result, I observed (rather than trapped) Snow Bunting flocks at the Newburgh trapping site on 23rd January 1992 and 14th December 1992 and established that, in agreement with trapping data, juvenile females were prevalent, forming 55% (n=80) and 62% (n=96) of the birds present on those occasions. Other age/sex categories were also present in similar proportions to that expected from trappings (as given in **Fig.4.2**). Thus, at low altitude sites, where the population is largely made up of the more transient age and sex categories (see **4.3**, **9.3** & Banks *et al.* 1991a) which may be more naive and hence less trap-shy, trapping data may give closer approximations of the true age/sex composition of birds using the site. This may mean that the difference in the relative abundance of adults and males between high altitude and low altitude sites is even greater than the previous chapter suggested.

Two factors possibly having major roles in determining the age/sex composition of Snow Bunting sub-populations at high altitude sites are (i) the age/sex composition of the whole wintering population (as established by breeding success), and (ii) the severity of winter experienced at the high altitude sites. If the former was more important we might expect a positive relationship between the annual relative abundances of males and females of the same age category. In contrast, if winter severity was more important, we might expect the proportions of juveniles and adults of a given gender to be positively correlated (because males are more likely to stay at high altitude sites following a snowfall - **5.3.5**). Although the abundance of adult females was negatively correlated with the abundance of juvenile females, the correlation between juvenile females and juvenile males was, at best, weak (and the proportion of adult males was not related to that of either adult females or juvenile males). Thus, although the data suggest that breeding success may play a bigger part in modifying between-year age/sex composition than winter weather, it is far from unequivocal. Other factors, related perhaps to the decision of whether or not to migrate from Iceland, may also be important. Clarification of this problem appears to require a much larger sample of annual age/sex composition estimates than the six presented here.

5.4.2 Altitudinal preferences at Cairn Gorm

Given that snow-free ground was available to them, Snow Buntings appeared to favour higher altitude parts of the Cairn Gorm study area compared to lower ground (see **5.3.4**). This was unlikely to be a result of avoiding trapping sites because birds were never trapped at the main observation area (CIFS) after April 1988. Similarly, I rarely saw Snow Buntings on unbaited (and hence not associated with trapping) parts of Levels 1 & 2 unless the 50% snow-cover line was low. My general impression, endorsed by **Fig.5.4**, was that Snow Buntings fed at or near the upper limit of snow-free vegetation whenever possible, or even higher if snow-cover was light (less than 2cm). Scraps discarded by humans may also have attracted some birds higher during complete snow-cover. On visits to the high altitude areas (Level 4), Snow Buntings could be found at all altitudes above about 1000m if snow-cover was incomplete.

The reasons why Snow Buntings prefer to feed on the highest parts of Cairn Gorm are likely to be similar to those given in the previous chapter. Also, the snow-line itself may be particularly attractive because thawing snow patches may irrigate the ground below, driving invertebrates and their larvae from the soil (pers. obs.). The vegetation also becomes shorter with increasing altitude, perhaps increasing the accessibility of the seed heads, and giving clearer views of approaching predators. Increasing height above the treeline may also reduce their vulnerability to forest edge or moorland predators such as Sparrowhawks and Merlins, while Stoats and Weasels are seldom seen above 1000m (pers. obs.). Finally, if there are cross-seasonal advantages to wintering on high ground, as speculated in the previous chapter, these are also likely to be emphasised on the Arctic Cairn Gorm-Ben Macdui plateau.

5.4.3 Differential migration following snowfalls

Difficulties in finding, counting and identifying birds easily at high altitudes prevented me from directly demonstrating the evacuation of Snow Buntings from Cairn Gorm at the onset of a snowfall. The Cairngorm Ski Area is but one corrie bordering a huge montane plateau over which Snow Buntings disperse widely during winter thaws. Occasional good views of large flocks on Level 4 (not included in the analyses above) during snow-free spells reinforced the impression that much larger numbers of females and unmarked birds were present during snow-free spells (**Table 5.7**). On these occasions the proportion of females in the flocks was comparable to that in coastal flocks (70-80% - see **Fig.4.2**), although these females were probably mainly adults (e.g. five out of six females captured on top of Ben Macdui on 1st February 1992). Snow Buntings were seldom seen or reported, however, in large numbers away from the Ski Area in severe weather, indicating that a large proportion of birds staying in the Cairngorms at these times were attracted to my baited areas. A substantial drop in overall numbers during snowfalls could therefore be inferred indirectly by increases in the relative abundance of marked birds, adults and males: these birds are unlikely to have *come up* from lower altitudes at the onset of snow.

Table 5.7. Estimates of flock composition of five large flocks seen well on Level 4 of the Cairn Gorm study area during mild periods.

Date	Number seen	Locality	Percentage that were: Females	Colour-ringed
12th November 1989	350	Cairn Gorm	80	1
5th December 1989	140	Cairn Gorm	-	30
25th January 1991	100+	Cairn Gorm	70	20
20th January 1992	125	Ben Macdui	-	20
1st February 1992	60	Ben Macdui	62	29

Facultative migration in response to deteriorating weather conditions or insufficient food supplies has been reported in a number of species (see for example Pulliam & Parker 1979, review by Gauthreaux 1982). The extent of facultative migration may, however, be influenced by the severity of the conditions. Mallards, for example, moved further south in colder winters (Nichols *et al.* 1983), and Yellow-rumped Warblers moved further south in late winter in response to climatic effects on food supplies (Terrill & Ohmart 1984). In the same way that partial or obligate migrants segregate across their winter ranges (see Gauthreaux 1982), it is often the case that the proportion of facultative migrants moving south in deteriorating conditions, or the distance they move, varies between age and sex categories (e.g. Alford & Bolen 1977, Bennett & Bolen 1978, Pattenden & Boag 1989). Further facultative movement by obligate migrants has also been noted in response to poor food supplies, and mainly occurs in socially subordinate individuals (Balph 1979, Terrill 1987).

Altitudinal migration, the movement of birds between neighbouring areas of different altitude, has been less frequently reported. Horvath & Sullivan (1988), however, reported that Yellow-eyed Juncos gradually returned to higher altitudes as winter ended, but again retreated to lower ground following a snowfall. Rabenold & Rabenold (1985) described altitudinal migration in the closely related Carolina Junco and found that the smaller and agonistically inferior females moved to lower elevations than males, especially in severe winters. Both these studies were conducted on species which bred in close proximity to their wintering sites. However, my results show that altitudinal migration within the non-breeding season also occurs in the absence of competition for breeding sites, although males, adults and birds with previous site experience (i.e colour-ringed) were again the least likely groups to abandon the high altitude sites when the weather deteriorated - they were often the only birds remaining following deep snowfalls or other

conditions forcing most birds to leave (**5.3.5**).

Without radio-tracking a large number of individuals over long periods of time, I clearly cannot fully describe the movement patterns of Snow Buntings visiting the Cairngorms. Certainly some birds remained at the same site for many weeks or months and some returned to the same site in further winters (see **9.3.4**). Others were sedentary at one site for long spells during one winter, then at another within the Cairngorms in subsequent winters. Further movements provided strong evidence of dramatic changes in wintering area between years. In contrast, 62% of birds moving to Cairn Gorm were seen on only 1-3 days. They may have been present for longer at higher altitudes on Cairn Gorm, but many must have moved on quickly (see **9.3.3**), perhaps as a result of worsening conditions.

To some degree, heritable factors may govern the likelihood and extent of migration (e.g. Biebach 1983, Berthold 1984), but Terrill (1987) showed that it can also be modified by other ecological and social conditions. Several intrinsic factors governing facultative migration, fidelity to a site, or nomadic versus sedentary behaviour have been suggested for a range of species. These include age (Townshend 1985), sex (Rabenold & Rabenold 1985, Pattenden & Boag 1989 and references therein) and rank (Balph 1979, Terrill 1987, Senar *et al.* 1992a). The next few chapters therefore consider the interplay between these factors, feeding efficiency and the accumulation and retention of energy reserves, and how they might contribute to the Snow Bunting's pattern of winter site use.

Chapter 6: FORAGING SUCCESS

6.1 INTRODUCTION

To survive the non-breeding season temperate passerines must avoid both starvation and being eaten (for reviews, see Real and Caraco 1986; Caraco & Lima 1987). They employ several strategies to achieve this, varying from territoriality and/or strict residency to long distance migration or nomadism. They will achieve maximum overwinter survival by choosing a wintering site (or sites) compatible with their physiological and competitive abilities. A number of studies have shown that age and sex categories may use different wintering strategies and habitats (reviewed in Gauthreaux 1982); this is often assumed to be at least partly due to differences in feeding rates (Gauthreaux 1982, 1988).

As an animal gets older its performance may improve in a number of ways which increase its ability to forage successfully. Part of this improvement may result from muscular or skeletal growth or development of the neurological system (reviewed in Marchetti & Price 1989), although in animals with determinate growth, such as birds, these changes may be limited to the first few weeks of life (Davies & Green 1976). In species where ossification of trophic structures is required for full function, maturation may take longer (e.g. the mussel-hammering beak of the Oystercatcher, Heppleston 1970; or the seed-crunching skull of the Hawfinch, Sims 1955). However, continued improvement in avian foraging success after the initial juvenile growth and maturation stage may be due to a second process, namely learning (Marchetti & Price 1989). This can be achieved in several ways. Firstly, a young bird may learn to capture or handle food more efficiently through practise or observation of other individuals (e.g. Sutherland *et al.* 1986, Jansen 1990, Desrochers 1992). Second, it gains knowledge of where or how to find food or how best to feed, either within its chosen habitat, or at a particular location (e.g. Piper & Wiley 1990a). Thirdly, its ability to feed in competitive situations may increase with experience through, for example, enhanced social skills, or increased success in agonistic encounters (Weatherhead & Teather 1987, Piper 1990). The effects of age on social dominance, and of social dominance on foraging success, are widely reported (reviews in Piper & Wiley 1989; Marchetti & Price 1989). Additionally sex differences in foraging success have been documented, and these too are usually attributed to the greater dominance rank of the larger gender (e.g. Greig *et al.* 1985, Sasvari 1992). Few, if any, studies have attempted to break down differences in foraging success among individuals to more than one of these sources despite the different implications each source might have on the age and sex ratio of birds found at a site, the quality of birds found at the site, or the importance of site fidelity.

Variation between individuals in intrinsic foraging skills (i.e. recognition of food patches, discovery of food within patches, food selection, capture success, handling times, etc.) can lead to differences in overall feeding rates. In many situations, especially if birds are feeding on one food source (e.g. Barnard 1980a, Puttick 1981), or are attracted to artificial food sources (e.g. Elgar 1987, Goldman 1980), it may be

convenient or sufficient to measure peck-rate or time spent feeding as an overall indication of foraging rate. The intrinsic foraging ability of an individual or group of individuals relative to others can, however, only be quantified if a number of extrinsic (i.e. environmental or social) variables are also considered.

The most commonly reported, and perhaps the most important, source of extrinsic variation in foraging rates is flock-size. As a result of such benefits as shared predator vigilance and reduced individual risk of predation (allowing individuals to reduce the time they spend vigilant), and faster patch location and evaluation (reviewed in Barnard & Thompson 1985; see also Hake & Ekman 1988, Benkman 1988), foraging rates tend to increase as flock-size increases (e.g. Powell 1974, Caraco 1979, Sullivan 1984). This increase can be tempered or even reversed, however, if food sources are limited or clumped (e.g. Feare & Inglis 1979, Elgar 1987, Saino 1994). Individuals feeding in central positions within groups also benefit because they are effectively screened from predators by their flock-mates and can therefore afford to increase foraging time in preference to vigilance (e.g. Goldman 1980, Jennings & Evans 1980). Further extrinsic influences affecting foraging success (or implicated by measured changes in vigilance) include distance from safety (negative affect on foraging rates - Barnard 1980c, Mayhew & Houston 1989; but opposite result recorded by Lima 1987 as birds foraged faster to minimise the time they were vulnerable to predators), priority of access (Black & Owen 1989), the presence of predators (Poysa 1987, Caraco *et al.* 1980), time of day (Ramenofsky *et al.* 1992) or prevailing weather (Caraco 1979). It is usually necessary to control for such influences on feeding rates before testing for intrinsic differences in ability between individuals.

It may also be the case that individuals can increase their overall foraging rates by foraging in the best situations. It is possible that more skillful birds (due to age or site experience) can feed faster (or more effectively) by selecting larger flocks, more central feeding positions, or more profitable stages within a flock's feeding bout than naive birds. However, competition for access to such favourable feeding situations is often reported: dominant birds tend to be found more frequently in favourable situations (e.g. in larger flocks, Owen & Dix 1986, Caraco *et al.* 1989; in safer sites, Schneider 1984, Hogstad 1988b; with priority of access, De Laet 1985). Rank-related access to food or feeding opportunities may therefore be as important a factor in determining overall foraging success as differences in intrinsic foraging abilities.

In this chapter I examine the factors that influence feeding rates in Snow Buntings, and in particular the contribution of age, sex and prior site experience to their feeding behaviour at an artificial feeding station. I report results from birds feeding in both potentially competitive and non-competitive situations (i.e. in flocks or alone) and present data on both peck-rates and the percentage of time spent feeding after correcting for environmental and social variables such as flock-size and priority of access to a foraging patch. Finally, I look at whether access to favourable feeding situations is related to gender, age or site experience, and whether these extrinsic factors are therefore likely to magnify or reduce differences in intrinsic foraging rates.

6.2 METHODS

All data used in this chapter were collected from December 1989 to March 1990 when Snow Buntings were attracted to an artificial feeding station at CIFS, consisting of a raised platform (3.0 x 1.5m) with a central arena (0.5 x 0.6m). I spread roughly 180g of pinhead oatmeal evenly over the arena before recording sessions, an amount sufficient to prevent noticeable depletion during the session. Arriving birds often settled on a 1m-high wire fence which surrounded the platform, allowing me to separate initial wariness upon arriving at the site from vigilance when feeding (because time budgets were only recorded from birds on the platform). Birds were observed from a vehicle stationed 15-30m from the feeding station. Snow Buntings were the only species recorded at the feeding station until late in the season when a few Chaffinches were also seen. No time budgets were taken if these were present.

Time budgets were obtained from both individually colour-ringed and unmarked individuals. It is unlikely that a bird could have been present for any length of time in a previous winter and remain unringed (and therefore unrecorded) because catches were made frequently so as to ensure a constantly high proportion of colour-ringed birds in the population (e.g. on average 65 ± 13% s.d. of the birds present at any one time in the 1988/89 winter were colour-ringed; n=67days). Almost 70% of newly caught birds were seen on three occasions or less, and only 23% of these were seen for more than a month after first trapping. Thirty birds previously ringed at other sites were also seen on Cairn Gorm during the 1989/90 winter and provided good evidence for the lack of site experience and transience of unringed birds: twenty of these were trapped within three observation days of their arrival on Cairn Gorm, while nine of the remaining ten were only ever seen less than three times on Cairn Gorm. In conclusion, most of the c35% of unringed birds present at any one time were probably transients that would not remain long at the site (see also **5.3.6** & **9.3.3**). Therefore an unringed individual, or an individual caught for the first time in the study winter, was considered to have had no previous site experience (calculated as the number of previous winters in which it had been seen on Cairn Gorm). Overall, of the marked birds providing time budgets in the 1989/90 winter, 71 had been ringed that winter, 37 the previous winter, and 8 in winter 1987/88, providing 53%, 42%, and 5.5%, respectively, of the time budgets from marked birds.

The age and sex of marked birds was determined in the hand using the criteria described in **3.2** and **3.5**. These methods were extended to age and sex unmarked birds in the field. I checked their reliability by comparing age/sex determinations of birds in the hand with age and sex determinations of the same birds when first resighted in the field. Altogether, 88% of individuals were correctly aged and 97% correctly sexed (n=49 & 209 respectively). Therefore any age/sex categorisation errors introduced by including the 17% of time budgets involving unmarked birds should be small.

6.2.1 Analysis of time budgets

A flock was defined as an aggregation of Snow Buntings whose nearest neighbours were no more than 5m away. This distance was chosen because it was less than the minimum distance to loafing areas (open ground with short, sparse vegetation rather than rank Heather which surrounded the feeding station), yet more than typical nearest neighbour distances (less than 2m) observed in flocks feeding in natural situations. Elgar *et al.* (1984) reported that House Sparrows feeding more than 1.2m apart acted independently. My definition for Snow Buntings, a species of more open environments, may therefore be appropriate.

Throughout this chapter, the term "feeding bout" refers to the activity of the flock as a whole, rather than to individual birds; it is defined as the period from the first bird of a flock alighting on the platform until either (i) the flock size increased or decreased by more than a factor of four in less than a minute, or (ii) all birds had left the platform. A flock-size change of fourfold or more was considered to herald the start of a new bout. My inability to record the exact arrival and departure times of all individuals whilst recording time budgets prevented me from selecting a smaller and more rigorous factor than four to indicate the start of a new bout. This value therefore represents a compromise between misclassifying the length of time for which individuals had been present, and underestimating the effects of a changing social environment (due to flock-size changes). However, in most analyses (**Table 6.1**), to help minimise such errors, time budgets during which the flock-size or the focal individual's nearest-neighbour distance changed by four-fold or more were discarded. Flock-size changes (of any magnitude) occurred in less than a quarter of the remaining time budgets.

Time budgets of up to one minute's duration (less if flushed, but always lasting 10s or more) were obtained from birds selected from the central arena. I attempted to choose an individually identifiable colour-ringed bird if possible, and a different bird in each consecutive time budget, but otherwise there was no conscious attempt to select particular individuals or types of individual. Colour-ringed birds should therefore have been sampled in a near random fashion, and in approximate proportion to the time they spent on the central arena.

Table 6.1. Criteria used for the selection of time budgets used in the main analyses. *A cross under DIST (x) indicates that no disturbance occurred during the time budget unless this instantaneously flushed the focal individual; PLST (x) indicates that focal individuals were on the central arena at the start of the time budget; 10S (x) indicates that all time budgets lasted at least 10s; PLEN (x) indicates that the focal individual was on the central arena at the end of the time budget; 10F (x) indicates that the focal bird spent at least 10s feeding; FFFC (x) indicates that the flock-size change between the beginning and end of the time budget did not exceed a factor of four (see text); 60S (x) indicates that the focal bird was present for a full minute; AGED (x) indicates that individuals which could not be classified as adults or juveniles were omitted from the analysis.*

Analysis	Results Section	DIST	PLST	PLEN	10F	FFFC	60S	AGED	Notes
Average time spent feeding	6.3.1	x	x	x	x	x			
Peck-rate when alone	6.3.2b	x	x	x	x	x		x	
Peck-rate when in flocks	6.3.2b	x	x	x	x	x	x	x	
% of time spent feeding (regression)	6.3.3a	x	x	x	x	x	x		a
% of time spent feeding (loglinear)	6.3.3b	x	x	x	x	x	x		
% occurrence in small vs large flocks	6.3.4a	x	x	x					b
% occurrence early vs late in feeding bout	6.3.4a	x	x	x					b
Likelihood of moving	6.3.4b	x	x	x	x	x	x		
On or off arena at end	6.3.4c	x	x	x		x	x		
Position within flock	6.3.4d	x	x	x	x	x			c

a Excludes time budgets when 0% or 100% of time was spent feeding

b Only includes colour-ringed birds

c Only includes flock-sizes of five or more birds

The behaviour and situation of the focal bird was recorded on a dictaphone for later transcription. Information transcribed and variables (capitals) derived from it are as follows:-

i) Identity of the focal bird, or AGE (juvenile or adult) and SEX (male or female) if it was unringed or if the legs were not seen sufficiently well to establish the bird's identity. AGE, SEX and prior EXPERIENCE at the site of focal colour-ringed birds were known from previous trapping and resighting data. AGE and EXPERIENCE were, of course, likely to be closely related because juveniles could not, by definition, have previous site experience. I therefore defined an extra variable, STATUS, for use in categorical analyses. The three categories of STATUS were juveniles, naive adults (those for which there was no evidence of their being present in previous winters) and experienced adults (those which had been seen in one or both of the two previous winters). EXPERIENCE was included as a continuous variable (range 0-2 winters prior site experience) in multiple regression analyses, but in other analyses as a categorical variable (no experience or some experience) because the sample of birds known to have been present in both the previous winters was small.

ii) Length of the flock's feeding bout (BOUT LENGTH, in minutes), length of the individual's time budget (TIMESEEN, in seconds), and time elapsed from the start of the flock's bout to the start of the individual's time budget (TIME FROM START, in minutes). TIME FROM START was also used in some analyses as a categorical variable by dividing the observations approximately equally into those beginning less than (early) or more than (late) two minutes after the flock's feeding bout had begun.

iii) Amount of time spent feeding (TIMEFEED, in seconds), number of pecks (PECKS), the PECK-RATE whilst feeding (i.e. PECKS/TIMEFEED, in pecks per second) and % TIME FEEDING (i.e. TIMEFEED/TIMESEEN). A bird was deemed to have stopped feeding if it didn't peck for over 5s, except in the case of more easily recognisable aggression when 2s was taken as the lower limit. Other activities included vigilance, loafing, walking, preening, bill-wiping, and stretching.

iv) FLOCK-SIZE (number of birds) and NEAREST NEIGHBOUR distance (in cm) for the focal bird, both taken as the average of their values at the start and end of the time budget. Additionally, in categorical analyses, time budgets were sub-divided by flock-size: birds alone, in small flocks (average of 1.5-3.5 birds) or large flocks (4 birds or more).

v) Average POSITION in the flock. Position in the flock was recorded at the start and end of each time budget (1=edge; 3=middle, i.e. surrounded by birds with no arc between neighbours (within 0.5m) greater than 90°; 2=intermediate between edge and middle). These scores were then added together; if the total was 3 or less, POSITION=1 (peripheral); if 4 or more, POSITION=2 (central).

vi) MOVEMENT, the distance travelled by the focal bird, estimated to the nearest 10cm with reference to the length of a Snow Bunting (c15cm) and the size of the central arena and

platform.

vii) Weather variables: ambient temperature (TEMPERATURE, °C), wind speed (WIND, in estimated Beaufort scale, 1-9), precipitation (PRECIPITATION; 1=absence, 2=presence). Unlike in other chapters which used daily means for weather variables (see **2.3**), these variables were recorded at the time of the time budget.

viii) Temporal variables: DAYs from 1st October and TIME of day.

Time budgets were discarded if they coincided with obvious human disturbance (loud noises, movements) unless these instantaneously flushed the focal individual. Most analyses (**Table 6.1**) were also limited to those time budgets where the focal individual was on the central arena at the end of the budget (indicating that its feeding motivation was still high). At least 30s elapsed between successive time budgets and a different bird was chosen each time if possible.

The above limitations resulted in the inclusion in the analyses of up to 1551 time budgets from 116 individually marked birds (median=5 time budgets, range 1-102), 310 time budgets from an unknown number of unmarked individuals (some of which may later have been marked), and an additional 40 time budgets from birds whose identity could not be determined. Additional selection criteria, described in **Table 6.1** and throughout **6.3**, substantially reduced the sample sizes for most analyses.

6.3 RESULTS

6.3.1 General activity during time budgets

On average, 82% of each time budget was spent feeding. Time not feeding was mostly spent vigilant, with other activities (loafing, preening, travel or aggression) occupying only 2.1% of the total time.

6.3.2 Peck-rate whilst feeding

6.3.2a Treatment of variables

PECK-RATE was computed for 1232 time budgets where ten seconds or more were spent feeding. Sample sizes allowed me to conduct separate stepwise multiple regression analyses for singletons and flocks (corresponding to absence and presence of competitors). FLOCK-SIZE, NEAREST NEIGHBOUR, TIME FROM START and BOUT LENGTH were normalised using a logarithmic transformation (log10). When peck-rates of flocks were examined, these variables were found to be significantly inter-correlated (all $P<0.001$, except logNEAREST NEIGHBOUR and logTIME FROM START which were not related). This was not a problem when carrying out the analysis on single birds, because only two of these variables were used (logBOUT LENGTH and logTIME FROM START) and the stepwise procedure only accepted one of

them. However, since predictor variables were correlated in the analysis of flock-feeding birds, a Principal Components Analysis was carried out on the logarithms of the four variables, producing two composite factors with loadings as follows:

FACTOR 1 = (0.57 x logTIME FROM START) + (0.53 x logBOUT LENGTH) - (0.22 x logNEAREST NEIGHBOUR) + (0.04 x logFLOCK-SIZE)

FACTOR 2 = (-0.68 x logNEAREST NEIGHBOUR) + (0.56 x logFLOCK-SIZE) + (0.17 x logTIME FROM START) + (0.08 x logBOUT LENGTH)

Factor 1 has large positive contributions of logBOUT LENGTH and logTIME FROM START, and therefore exhibits small values at the start of short bouts and large values at the end of long bouts. It is referred to as BOUTTIME. Factor 2, however, has large positive contributions of logFLOCK-SIZE and large negative contributions of logNEAREST NEIGHBOUR. The factor is thus a measure of flock density, and is subsequently referred to as DENSITY. The two factors explained 51% and 30%, respectively, of the total variance between the four variables and were found to explain more variation in peck-rates than any of their components; they were therefore used in the analyses of flock-feeding birds in place of the four original variables.

6.3.2b Multiple regression of peck-rates whilst feeding

The variables related to the number and proximity of birds and the timing of the time budget (DENSITY and BOUTTIME for flocks, logBOUT for singletons) accounted for most of the explainable variance in peck-rate when birds were feeding either alone or in flocks (**Table 6.2**). Peck-rates were higher for birds in more central positions within flocks, and seasonal and environmental variables were also significant (although explaining only minor amounts of variation).

More interestingly, however, peck-rate whilst feeding increased with prior experience if alone, or age if in a flock. On average, solitary birds pecked 9% faster if they were experienced than if they were spending their first winter at the site, while in flocks adults fed 8% faster than juveniles (values calculated from the regression coefficients of the multiple regressions). There was no overall difference in peck-rates between the sexes in either analysis.

AGE and EXPERIENCE were, as expected, highly correlated ($P<0.001$). I therefore repeated the multiple regression analyses without including the predictor variables AGE or EXPERIENCE, and examined the residuals grouped according to STATUS. Residual peck-rate was strongly related to STATUS (**Fig.6.1**): both age and previous site experience had independent positive effects on peck-rate and these effects were very similar in magnitude (approximately 3 pecks/min, a difference of 4-6%) in both solitary and social situations (oneway ANOVA for solitary birds: $F_{2,504}=5.1$, $P=0.006$; for birds in flocks, $F_{2,722}=4.5$, $P=0.011$).

Table 6.2. Factors influencing peck-rate in wintering Snow Buntings. *Stepwise multiple regressions of peck-rates were carried out separately for birds feeding a) alone (n=507 time budgets), or b) in flocks (n=725). In (a) the independent variables considered were AGE, SEX, EXPERIENCE, logBOUT LENGTH, logTIME FROM START, TEMPERATURE, WIND, PRECIPITATION, DAY and TIME. In (b) AGE, SEX, EXPERIENCE, POSITION, TEMPERATURE, WIND, PRECIPITATION, DAY and TIME were included along with the two Principal Components, BOUTTIME and DENSITY (see text). Significant variables are listed in order of inclusion in the equation.*

DEPENDENT VARIABLE	INDEPENDENT VARIABLES entered in the equation	Partial correlation coefficient a	Proportion of variation explained (r^2)
a) Solitary individuals			
PECK-RATE	logBOUT LENGTH	-0.34 ***	0.125
	WIND	0.15 ***	0.020
	EXPERIENCE	0.11 **	0.013
		Total r^2 =	0.157
b) Individuals in flocks			
PECK-RATE	DENSITY	0.27 ***	0.088
	BOUTTIME	-0.21 ***	0.080
	POSITION	0.12 ***	0.012
	WIND b	0.07 n.s.	0.010
	AGE	0.11 **	0.008
	DAY	-0.10 **	0.004
	TEMPERATURE	0.08 *	0.006
		Total r^2 =	0.208

a * P<0.05, ** P<0.01, *** P<0.001

b Later removed from the equation

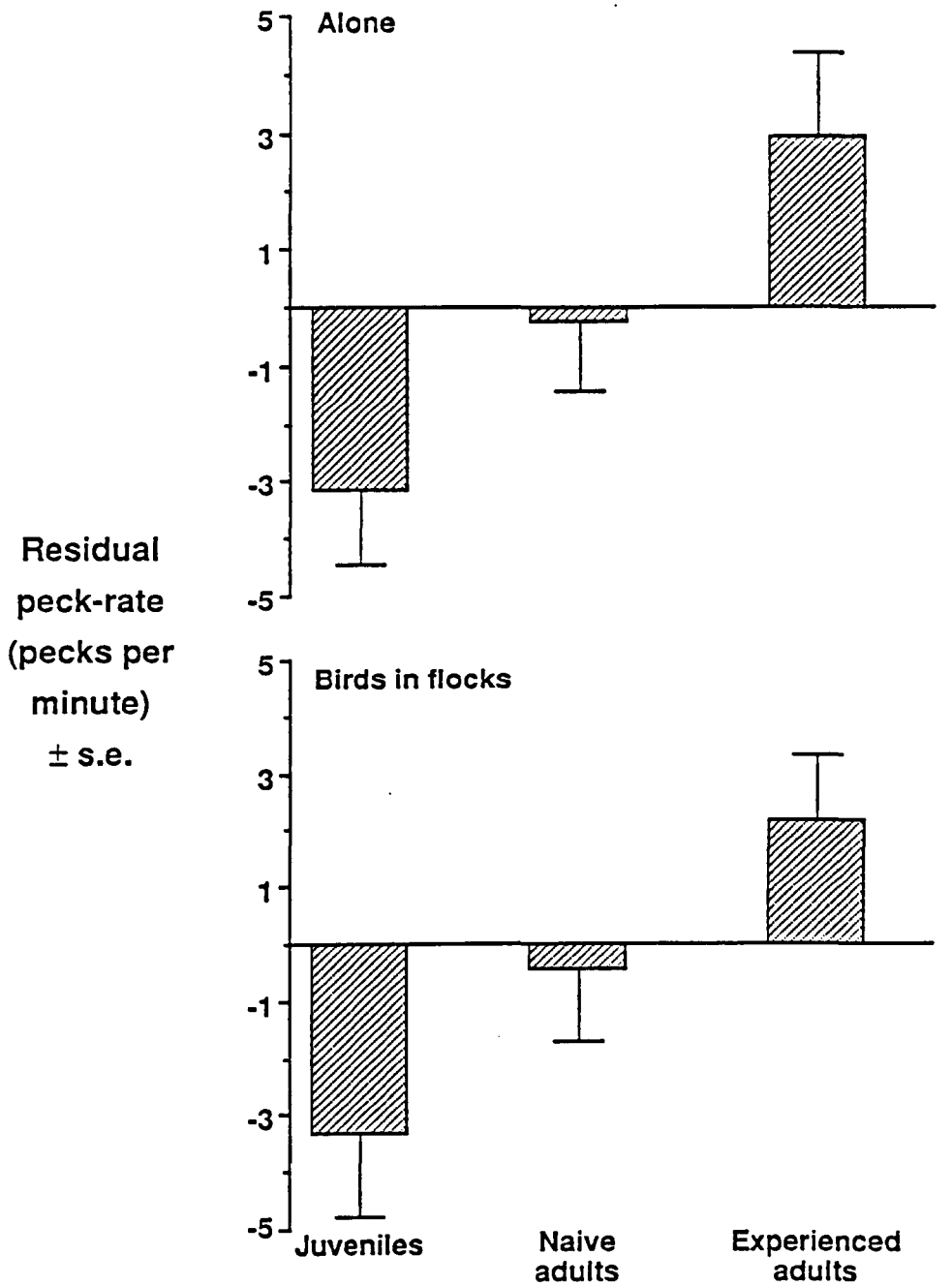


Fig.6.1. Variation in mean residual peck-rate (± s.e. bar) between Snow Buntings of different age and prior site experience. *Residuals were calculated from the multiple regression analyses of peck-rates shown in* ***Table 6.2****, but excluding the predictor variables AGE and EXPERIENCE. Experienced adults had significantly higher peck-rates than younger and less experienced individuals both when feeding alone (above) or in flocks (below).*

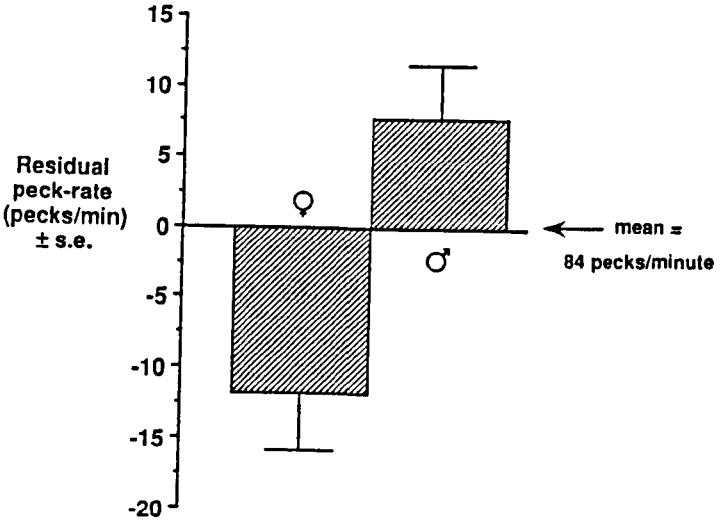
The sampling procedure under-represented time budgets taken from large flocks relative to the amount of time individuals spent in such flocks because I could only record one time budget at a time. Therefore, any influences on peck-rates occurring only in larger flock-sizes might not have been detected by the previous analysis. I therefore examined the 40 multiple regression residuals obtained from birds in larger flock-sizes (average flock-sizes of at least 12 birds). I again calculated the residuals from a multiple regression which excluded AGE and EXPERIENCE, but corrected for the overall combined effect of these variables by subtracting the mean residual for each STATUS category (calculated from all 725 time budgets - see **Fig.6.1**) from the 40 'large flock' residuals. This then allowed me to test whether or not the effect of STATUS was exaggerated in large flocks. As competition was probably greatest in these large flocks, I again included SEX as a possible influence and analysed the residuals using ANOVA. Overall, the predicted mean peck-rate (84.0 pecks/minute) was close to the observed mean peck-rate (82.8 pecks/minute, s.e.=3.2) in these time budgets, indicating that the model was fairly robust. There were no additional effects of STATUS on residual peck-rate in large flocks ($F_{2,34}$=0.05, n.s.) but SEX was important. Males had significantly greater peck-rates than females when the other explanatory variables had been taken into account ($F_{1,34}$=11.0, P=0.002; **Fig.6.2**): in large flocks they pecked approximately 27% faster than females.

6.3.2c Individual improvement of foraging success over the winter

The higher feeding rates of adult and experienced Snow Buntings could be due to either changes within individuals as they got older or more experienced, or to differential return rates (i.e. those individuals having relatively low peck-rates in their first winter at the site being less likely to return in subsequent winters, leading to an apparent higher mean peck-rate in those that did return). To test for evidence of increasing peck-rates with experience within individual birds, I looked for trends within one winter. For this analysis, I selected individuals which had been time budgeted on five days or more, spread over at least a 10-day period. This resulted in a sample of 26 birds when feeding in flocks, and seven birds feeding alone. For these birds residual peck-rates from the analyses above were plotted against date to obtain a regression slope. The sample sizes were only sufficient to compare slopes between EXPERIENCE categories (i.e. juveniles and naive adults were grouped together).

Neither the mean number of time budgets per individual, nor the mean timespan over which these time budgets were measured, differed between inexperienced (n=18) and experienced (n=15) birds (P>0.1). However, 72% of the inexperienced Snow Buntings showed *increased* foraging success with date (i.e. the regression slopes were positive) as opposed to only 40% of the experienced birds. After taking into account the gradient of the slopes, this difference was significant (**Fig.6.3**; Mann-Whitney U-test, z=2.33, P=0.019). Thus inexperienced birds tended to show an increase in peck-rates with time spent at the site, whereas no additional improvement was noticeable in birds that had been present in previous winters.

Fig.6.2. Comparison of residual peck-rates (± s.e.) of male and female Snow Buntings in large flocks. *Data was derived from the multiple regression model predicting peck-rates of birds in flocks (Table 6.1), but omitting the predictor variables SEX, AGE and EXPERIENCE. I only selected residuals from birds in flock-sizes of 12 or more. After controlling for other variables, males had higher peck-rates than females.*



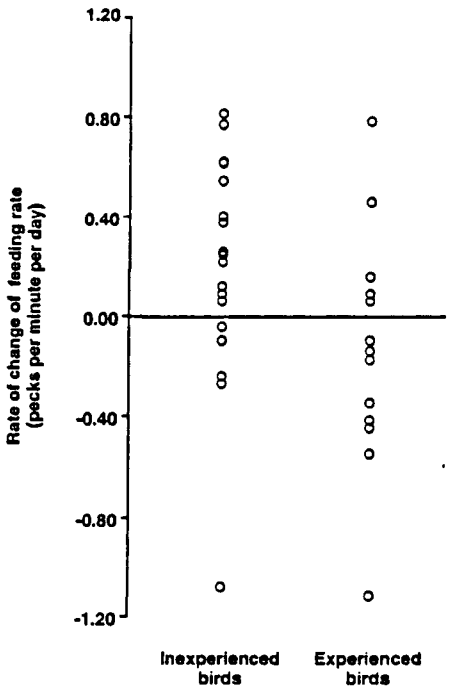
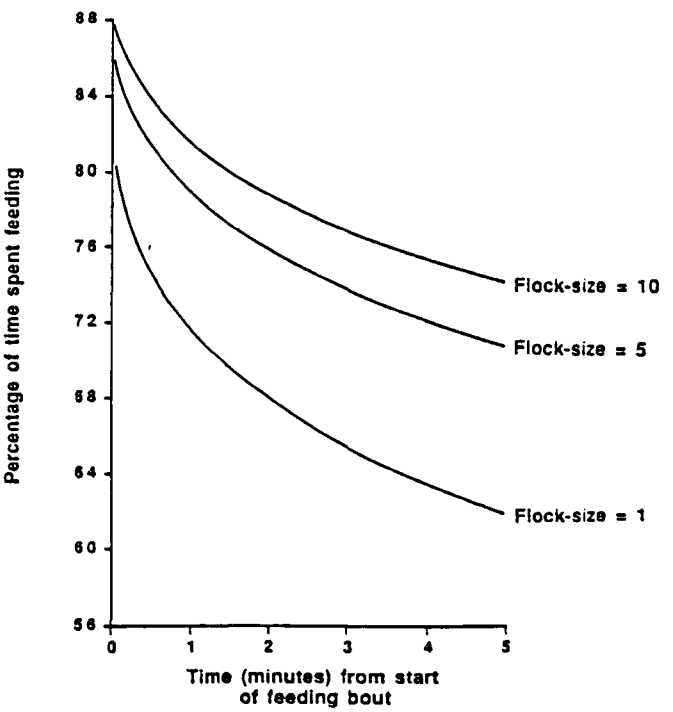


Fig.6.3. The rate of change of peck-rates per day of inexperienced and experienced Snow Buntings. *Values are the slopes of the regression of residual peck-rate (pecks per minute) against days from the first recorded time budget. Only birds sampled on five or more days over at least a 10-day period were included. Inexperienced birds showed a greater increase in peck-rate with time than experienced birds.*

Fig.6.4. Average percentage of time devoted by Snow Buntings to feeding, against time since the flock started the feeding bout, plotted for three different flock-sizes (n=660 time budgets). *Observations where either all or none of the entire time was devoted to feeding were not considered. Lines are derived from the multiple regression model summarised in Table 6.3.*



6.3.3 Percentage of time spent feeding

Higher peck-rates whilst feeding are, in isolation, insufficient evidence that adult, experienced or male Snow Buntings foraged more efficiently than their counterparts. Juvenile, inexperienced or female birds may have been able to offset the short-term deficit by spending more of their available time feeding. I therefore examined the factors influencing how long focal individuals spent feeding during time budgets.

6.3.3a Multiple regression of time spent feeding

The percentage of time spent feeding in a time budget was not normally distributed because there was a large number of cases where either none or all of the time was spent feeding (3.1% and 53.9% of time budgets, respectively). The first approach was therefore to omit those budgets where all or none of the time was spent feeding, and to transform (log10 [% TIME FEEDING/{100-% TIME FEEDING}]) the remaining cases to obtain an approximate normal distribution. These cases were then used in a multiple regression analysis with transformed % TIME FEEDING as the dependent variable.

Altogether, 660 time budgets remained after omitting those where all or none of the time was spent feeding. % TIME FEEDING, in concordance with PECK-RATE, decreased with time from the start of the bout and increased with flock-size (**Table 6.3**). The effect of these variables was greatest early in the bout and in small flocks (**Fig.6.4**). AGE, SEX and EXPERIENCE were not significant, but this was perhaps not expected because I omitted a large number of cases where the whole time budget was spent feeding (over half the total sample). These may have been biased towards particular age or sex categories.

Table 6.3. Factors influencing the percentage of time spent feeding by Snow Buntings. *Stepwise multiple regression was performed on the transformed percentage of time spent feeding (n=660 time budgets). Explanatory variables considered were AGE, SEX, EXPERIENCE, logBOUT LENGTH, logTIME FROM START, logFLOCK-SIZE, POSITION, TEMPERATURE, WIND, PRECIPITATION, DAY and TIME. Only significant variables are listed, in order of entry to the model. Cases where the entire time was spent either feeding or not feeding were omitted (see text).*

DEPENDENT VARIABLE	INDEPENDENT VARIABLES entered in the equation	Partial correlation coefficient a	Proportion of variation explained (r^2)
% TIME FEEDING	logTIME FROM START	-0.27 ***	0.075
	logFLOCK-SIZE	0.12 **	0.014
		Total r^2 = 0.089	

a ** P<0.01, *** P<0.001

6.3.3b Loglinear analysis of time spent feeding

As an alternative method of examining variation in the amount of time devoted to feeding, I looked at the possible influence of various situational or individual factors on whether or not *most or all* of a focal individual's time budget was spent feeding. This method of analysis was able to use the whole spectrum of time budgets (0-100% of time spent feeding), but was necessarily restricted to those which lasted for an entire minute. I then classified them according to whether or not 90% of the time was spent feeding. This criterion distinguished between those time budgets where the focal bird had one or less brief pauses from feeding (possibly due to chance events), and those where it stopped more than once or for a longer spell (feeding more likely to be voluntarily curtailed or inhibited/prevented by conspecifics). I then employed loglinear models to test for effects of FLOCK-SIZE (categorised as solitary, 2-3.5 birds, or four or more birds, see **6.2.1**) and TIME FROM START (early and late, see **6.2.1**), and, after controlling for these variables, to look for differences between the age, experience and sex categories.

Loglinear analysis indicated that both time from the start of the flock's feeding bout (X^2_1=74.0, P<0.001) and flock-size (X^2_2=49.4, P<0.001) affected the likelihood of spending 90% or more of the time budget feeding (**Fig.6.5**). As expected from the previous analysis, the focal bird was more likely to spend most of its time feeding in early time budgets and/or in large flocks.

Comparisons of time spent feeding were then made between the sexes within an age category and between ages within a sex category (**Fig.6.6, Table 6.4**); these comparisons also included the effect of flock-size, while early and late time budgets were analysed separately.

Table 6.4. The relationships between the likelihood of a Snow Bunting spending at least 90% of a time budget feeding, flock-size and age/sex category. *Loglinear analyses were conducted on time budgets begun (a) early (within two minutes of the start of the flock's feeding bout), and (b) late (more than two minutes after the start of the bout). Values given are the probability that the interaction between the given variables (left-hand column) had no effect on the distribution of time budgets between time-feeding, flock-size and age/sex categories (as depicted by* ***Fig.6.6****) once insignificant interaction terms were omitted from the model. Two-variable interaction terms are given only when there was no significant 3-way interaction between all three variables.*

Comparison between:	Age categories		Sex categories	
	Female	Male	Juvenile	Adult
Interaction:				
a) Early				
Time-feed*flock-size*age/sex	n.s.	n.s.	n.s.	n.s.
Time-feed*flock-size	0.007	<0.001	0.007	<0.001
Time-feed*age/sex	n.s.	0.004	0.030	0.010
Flock-size*age/sex	0.014	n.s.	0.011	n.s.
b) Late				
Time-feed*flock-size*age/sex	0.037	n.s.	0.017	n.s.
Time-feed*flock-size	-	0.001	-	<0.001
Time-feed*age/sex	-	n.s.	-	n.s.
Flock-size*age/sex	-	0.001	-	0.002

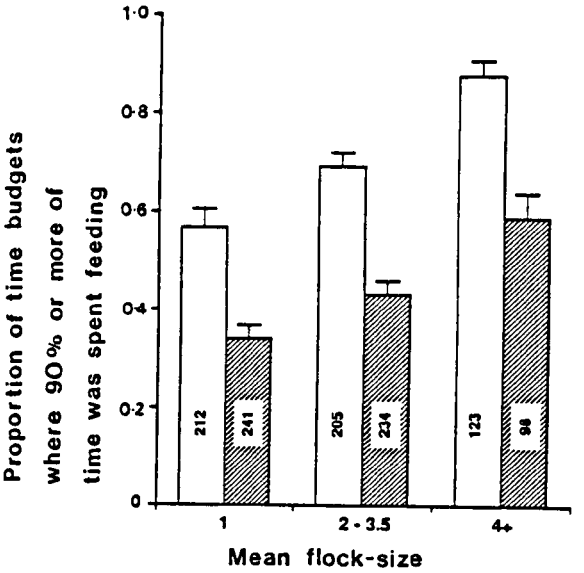


Fig.6.5. Proportion of Snow Bunting time budgets where 90% or more of the time was spent feeding in relation to flock-size and time from the start of the flock's feeding bout. *Early time budgets (open) were begun within two minutes of the beginning of a flock's feeding bout, late time budgets (hatched) were begun thereafter. Sample sizes (number of time budgets) are given on bars.*

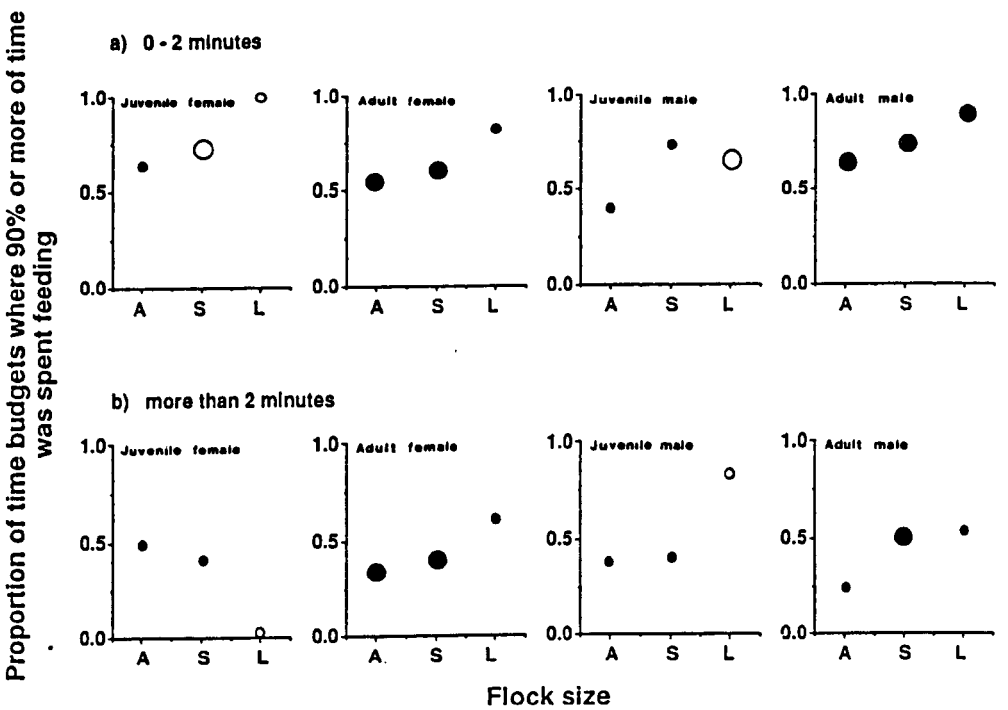


Fig.6.6. Proportion of time budgets where 90% or more of the time was spent feeding for different age/sex categories and flock-sizes of Snow Bunting in (a) early time budgets (begun within two minutes of the flock beginning a feeding bout), and (b) late time budgets (those begun more than two minutes after the beginning of a feeding bout). *Data are categorised by whether the bird was alone (A), in a small flock (1.5-3.5 birds, S) or a large flock (4 birds or more, L). Small open circles: n=3-5 time budgets; large open circles: n=10-20; small filled circles: n=21-50; large filled circles: n=51-100. Results of comparisons between pairs of age/sex categories are given in* ***Table 6.4.***

In time budgets from early in a feeding bout, birds of all age/sex categories were again more likely to spend more time feeding when in flocks (**Table 6.4, Fig.6.6**). The effect of most interest here, however, is that of age or sex category on time allocated to feeding. Three of the four pairwise comparisons were significant (the 'Time-feed*age/sex' interaction in **Table 6.4**). Adult males were more likely to devote 90% or more of the time to feeding than either adult females or juvenile males, whilst juvenile females were more likely to do so than juvenile males (although the sample sizes for the former were small, especially in large flocks; **Fig.6.6**). The three significant flock-size by age/sex category interactions were due to the distribution of time budgets involving juvenile females between flock-sizes; time budgets of these birds in large flocks were under-represented compared to the other age/sex categories, possibly due to sampling biases (but see **6.3.4a**).

In time budgets from late in a bout, pairwise analyses between adult females, adult males and juvenile males again indicated a strong positive influence of flock-size on the amount of time devoted to feeding (**Table 6.4, Fig.6.6**). However, none of these three age/sex categories were significantly more likely than the others to devote most of the time budget to feeding. Pairwise analyses between juvenile males and females, and between juvenile and adult females were complicated by significant 3-way interactions between time spent feeding, age/sex category and flock-size (**Table 6.4**). This may again have been due, in part, to poor representation of time budgets from juvenile females in large flock-sizes, relative to the other age/sex categories. Examination of **Fig.6.6**, however, indicates it may also have been partly caused by a reversal of the effect of flock-size on time spent feeding in late juvenile female time budgets. In support of this, juvenile females were found to both spend more time feeding when alone (X^2_1=4.96, P<0.05), and have a tendency to spend less time feeding when in large flocks (Fisher exact P=0.13), than the other age/sex categories combined.

Similar results were obtained when EXPERIENCE was used in the models instead of AGE. Experienced males were more likely to spend 90% or more of their time feeding than either experienced females (X^2_1=6.31, P=0.01) or inexperienced males (X^2_1=15.4, P<0.001) early in the bout. However, they were less likely to spend most of their time feeding in late bouts than experienced females, although the difference was reduced in large flocks (3-way interaction: X^2_2=7.14, P=0.03). Experienced females were also more likely to spend 90% or more of their time feeding than inexperienced females in the later part of a feeding bout (X^2_1=11.9, P<0.001).

To summarise, in general birds were able to spend more time feeding when in larger flocks, although the opposite trend was apparent in juvenile females later in a flock's feeding bout. Birds devoted more time to feeding in the early part of a feeding bout. This was especially true of adult males, which were able to spend more time feeding then than either adult females or first-winter males; no such difference was seen later in the bout.

6.3.4 Access to food and feeding positions

Several of the previous analyses indicated the strong influences of flock-related variables (flock-size, nearest-neighbour distance and position within a flock) and the relative timing of a time budget in determining peck-rate and the percentage of time allocated to feeding (**Figs.6.1, 6.4 & 6.5; Tables 6.2, 6.3 & 6.4**). Similarly, the significant interactions between flock-size and age/sex category in **Table 6.4** indicated that the distribution of individuals amongst different flock-sizes may be non-random (although the preferential selection of colour-ringed birds may have influenced this result). Individual feeding rates may therefore have been influenced to a greater extent by the choice of flock to join, and where and when to feed, than by individual attributes such as age, sex or experience. Hence, in this next section I examine the data for patterns of flock membership, feeding priority, ability to remain feeding, and position within a feeding flock in relation to age, sex and site experience.

6.3.4a Flock-size choice

Firstly, were experienced birds, adults or males more frequent in larger flocks? Difficulties arose from the original selection of time budgets because I chose colour-ringed birds in preference to unmarked birds, and on average more adults and males than juveniles or females were colour-ringed at any one time (as a result of their greater site tenacity, see **5.3.5, 9.3.2, 9.3.3**). Hence these would tend to be chosen earlier during bouts and more often as flock-size increased. To counteract this problem I therefore selected only time budgets from colour-ringed birds. The sample was increased, however, by relaxing the restrictions on choice of time budgets (**Table 6.1**), since subsequent events during the minute would not have affected my initial choice of focal bird or the flock-size present at the start of the individual's time budget.

Loglinear analysis of the 1548 time budgets for which relevant data were available revealed a significant interaction between FLOCK-SIZE (in this case the relevant value for FLOCK-SIZE was the flock-size at the start of the time budget, not the average between the values at the start and end of the time budget), SEX and STATUS (X^2_4=17.3, P=0.002). This was mainly due to a decrease in frequency of inexperienced females as flock-size increased (**Fig.6.7**). Indeed, if the analysis was run simply between sexes, or between experience categories, males and experienced birds were found more often than their counterparts in large flocks as opposed to singly (SEX: X^2_2=16.1, P<0.001; EXPERIENCE: X^2_2=9.37, P=0.009).

6.3.4b Priority of access

To find out whether males, adults or experienced birds were able to feed earlier in flock feeding bouts than their counterparts, I again restricted the analysis to colour-ringed birds and included the larger data set (as in **6.3.4a**). Early time budgets were again those begun within two minutes of the start of the flock's feeding bout.

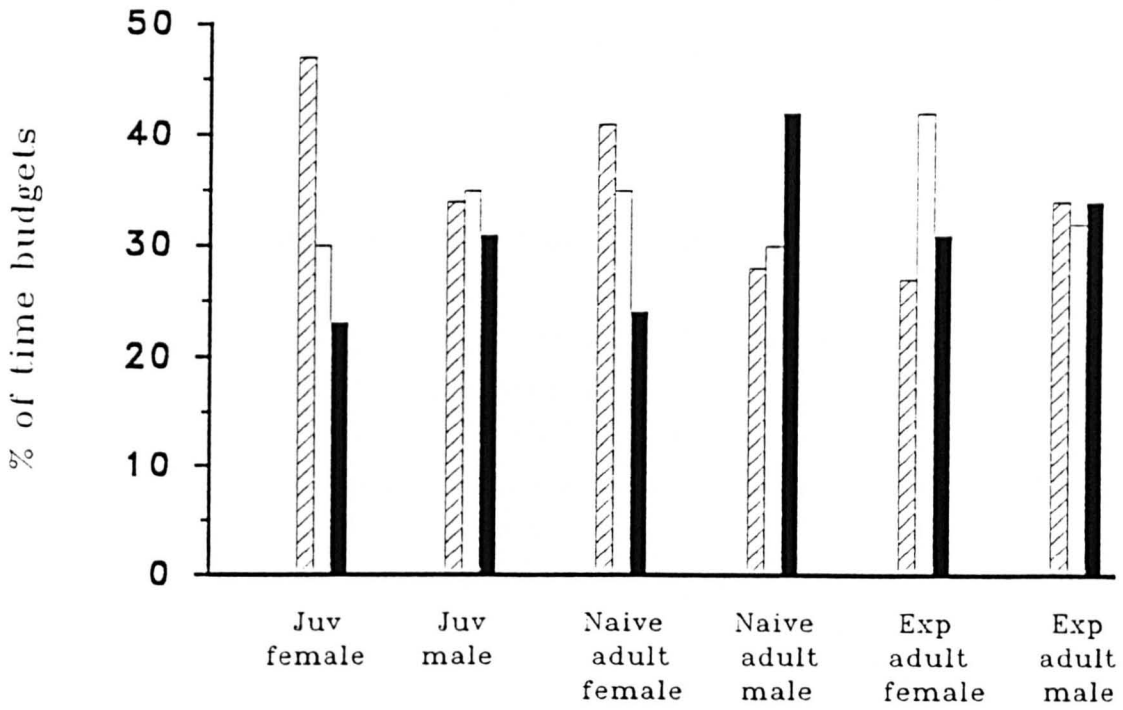


Fig.6.7. Variation in the distribution of Snow Bunting time budgets amongst flock-sizes in relation to age, site experience and sex. *Hatched bars represent the percentage of time budgets taken from initially solitary individuals, blank bars those from birds initially in flocks of 2-3, and filled bars those from birds in larger flocks. Sample sizes are 146 time budgets from juvenile females, 192 from juvenile males, 272 from naive adult females, 127 from naive adult males, 276 from experienced adult females and 456 from experienced adult males.*

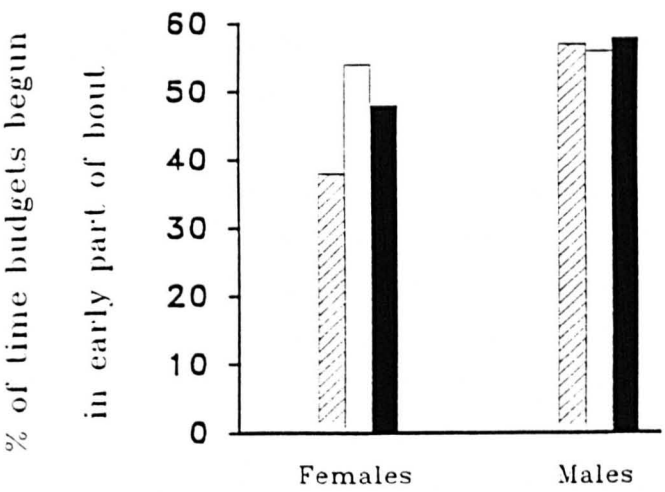


Fig.6.8. The influence of age, prior site experience and sex on the percentage of Snow Bunting time budgets begun early in a flock's feeding bout (within two minutes), rather than later. *Hatched bars represent juveniles, blank bars naive adults, and filled bars experienced adults. Sample sizes are left to right 146, 273, 276, 192, 127 & 458 time budgets.*

In the initial loglinear model, the TIME FROM START*SEX*STATUS interaction approached significance (**Fig.6.8**; X^2_2=4.96, P=0.08), mainly because females (especially juveniles) were less frequent early in time budgets (TIME FROM START*SEX, X^2_1=13.6, P<0.001). No difference between the experience categories in the timing of male time budgets was evident (**Fig.6.8**).

6.3.4c Ability to remain in a feeding position

Given that an individual gained access to the central arena, how likely was it to maintain this position throughout the minute? I did not measure how long an individual stayed on the arena, but I did estimate how far the focal bird moved during its time budget and whether or not it was still on the central arena at the end of the time budget. Movement or displacement of the focal individual might indicate greater difficulty in sustaining its place in a feeding flock.

To look at whether the amount of movement varied between age, sex or experience categories, I selected the 1147 time budgets that lasted for a whole minute when the focal individual was still on the arena at the end of the minute. I categorised time budgets as showing movement only if the focal bird moved 30cm (approximately two bird lengths) or more during the minute. Shorter movements than this were categorised as no movement because birds often shuffled slowly forward as they fed, irrespective of any obvious interference from competitors.

Birds were more likely to move when in flocks, especially larger flocks, but movement was independent of time from the start of the flock's feeding bout (**Fig.6.9**; for FLOCK-SIZE, loglinear X^2_2=75.7, P<0.001; TIME FROM START, X^2_1=1.39, P=0.24). I therefore retained the three flock-size categories when assessing the influences of age, sex and site experience on the likelihood of moving.

The loglinear model incorporating MOVEMENT, FLOCK-SIZE and SEX indicated a significant interaction between all three variables (3-way interaction term, X^2_2=8.12, P=0.018). Examination of **Fig.6.10** suggests that this was because males were slightly more likely to move if alone, but less likely to have moved in a large flock. A similar model incorporating STATUS showed no such 3-way interaction (X^2_2=3.52, P=0.48) nor an overall effect of STATUS (MOVE*STATUS: X^2_2=3.10, P=0.21).

Some focal individuals left the arena during the time budget, but stayed on the feeding platform, presumably waiting for a chance to feed again. Perhaps this was a result of competition for space. I again tested whether different age, sex or experience categories were more likely than their counterparts to show this behaviour. Once more, I selected time budgets which lasted for a whole minute, but in these analyses also included time budgets where the focal individual was on the feeding platform (perhaps indicating a willingness to continue feeding) but not necessarily on the central arena at the end of the minute (n=1231). As expected, focal birds were more likely to move off the central arena during the time budget if the

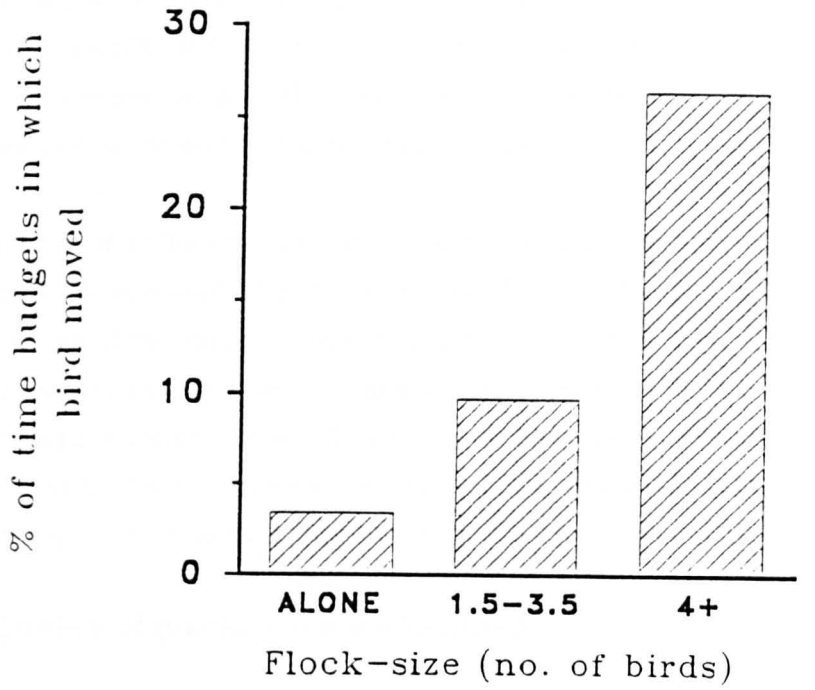


Fig.6.9. The impact of flock-size on the percentage of Snow Bunting time budgets in which the focal bird moved at least 30cm. *Sample sizes are (left to right) 470, 465 & 212 time budgets.*

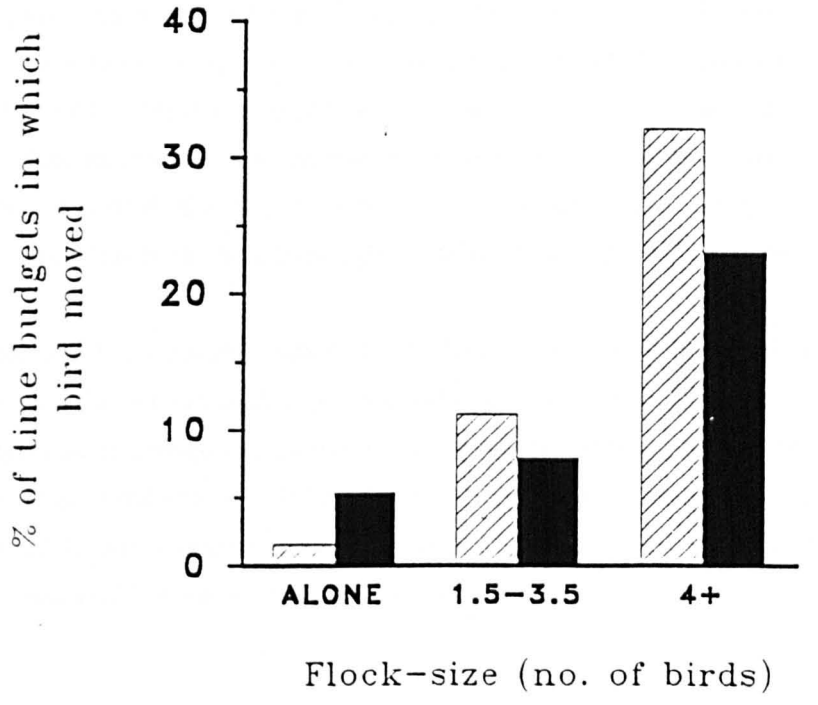


Fig.6.10. The percentage of Snow Bunting time budgets in which the focal bird moved at least 30cm, in relation to flock-size and gender (hatched bars represent females, filled bars males). *Sample sizes are (left to right) 248, 223, 267, 201, 78 & 135 time budgets.*

average flock-size was large, but showed no tendency to leave the arena in early versus late time budgets (**Fig.6.11**; FLOCK-SIZE, loglinear $X^2_2=22.7$, $P<0.001$; TIME FROM START, $X^2_1=1.78$, $P=0.18$). I therefore again retained the three flock-size categories when assessing the effects of age, sex and experience on whether the focal individual was on or off the arena at the end of its time budget.

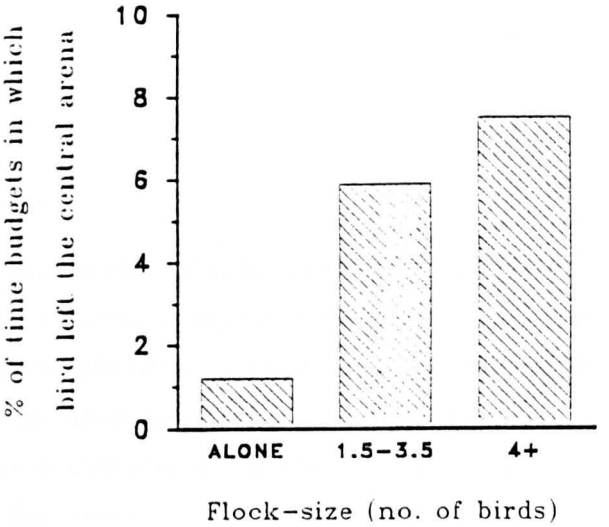
When including all three flock-size categories, loglinear analysis failed to pick up significant differences between age, sex or experience categories (all $P>0.11$). However, if only birds in large flocks (i.e. most likely to be forced off the arena as a result of competition) were considered, older birds, and to a lesser extent experienced birds, were more likely to remain on the central arena at the end of the minute than juveniles (**Fig.6.12**; $X^2_2=6.40$, $P=0.04$). There was no evidence that this effect differed between the sexes (PLACE.END*SEX*STATUS: loglinear $X^2_2=3.14$, $P=0.21$) or that gender itself affected the focal bird's chances of being on the central arena at the end of the minute (PLACE.END*SEX: $X^2_1=0.99$, $P=0.32$).

6.3.4d Quality of position within the flock

Finally, were particular categories of birds more likely to be found in better feeding positions within flocks than others? Focal birds were only recorded in central positions within flocks (POSITION=2, see **6.2.1**) in flock-sizes of five or more, so I limited the analysis to the 255 time budgets from these larger flocks. As I expected that the likelihood of being in a central position within the flock would increase rapidly with flock-size, I again categorised FLOCK-SIZE, but on this occasion flocks of 5-7 birds were 'small', 7.5-10 birds 'medium', and more than 10 birds 'large'. Loglinear analysis of POSITION with FLOCK-SIZE and TIME FROM START justified this expectation: focal birds were in central positions in only 11% of time budgets taken from small flocks, but this rose to 27% and 58% in medium and large flocks respectively (POSITION*FLOCK-SIZE: $X^2_2=43.2$, $P<0.001$). Position within a flock did not appear to be influenced by time from the start of the flock's time budget (POSITION*TIME FROM START: $X^2_1=0.21$, $P=0.65$).

A full loglinear model incorporating both SEX and STATUS with POSITION and FLOCK-SIZE indicated that SEX did not affect a bird's feeding position within a flock (POSITION*SEX: $X^2_1=0.18$, $P=0.67$; no significant higher order interactions). However, there was some tendency for older and more experienced birds to be found in central positions (POSITION*STATUS: $X^2_2=4.70$, $P=0.095$). Indeed this relationship, shown in **Fig.6.13**, was significant ($X^2_2=7.14$, $P=0.03$) if the near significant interaction between FLOCK-SIZE and STATUS was not removed from the model.

Fig.6.11. The influence of flock-size on the percentage of Snow Bunting time budgets in which, at the end of one minute, the focal individual remained on the platform but had left the central arena (as opposed to being both on the platform *and* on the central arena). *Sample sizes (left to right) are 481, 510 & 240 time budgets.*



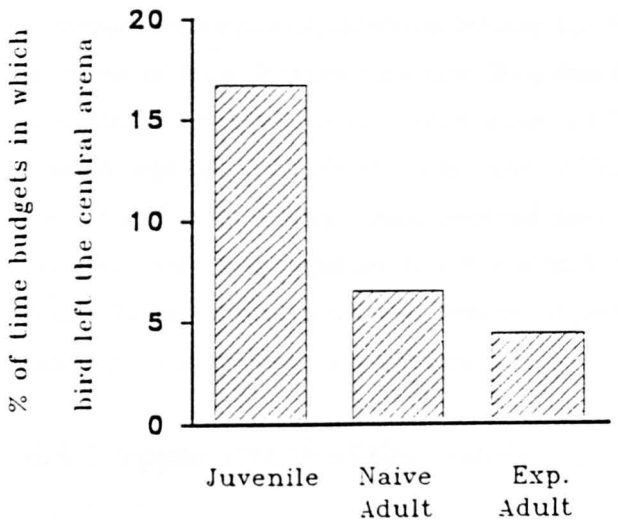
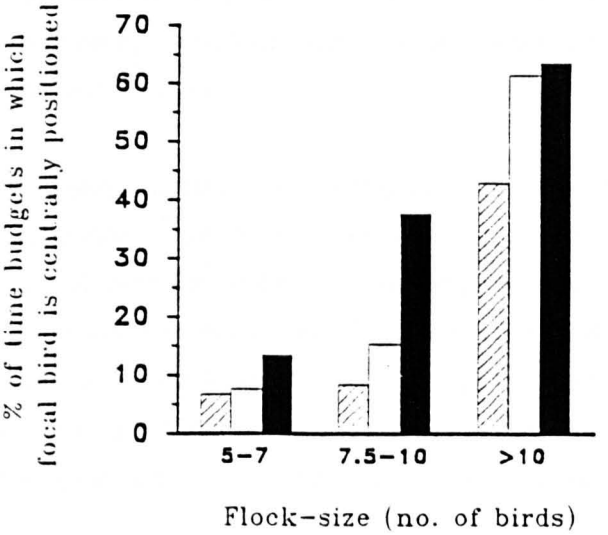


Fig.6.12. The percentage of Snow Bunting time budgets from large flocks (4+ birds) in which the focal individual remained on the platform but had left the central arena, arranged by STATUS. *Sample sizes (left to right) are 48, 77 & 114 time budgets.*

Fig.6.13. The percentage of Snow Bunting time budgets in which the focal individual was centrally positioned within the flock (as opposed to peripheral), in relation to flock-size and STATUS (hatched bars represent juveniles, blank bars are naive adults, and filled bars are experienced adults). *Sample sizes are (left to right) 30, 40, 67, 12, 13, 37, 14, 13 & 22 time budgets.*



6.4 DISCUSSION

6.4.1 Influences on feeding efficiency

After controlling for flock- and feeding bout related variables (flock-size, density, position within the flock, bout-length and time into the bout), adults and/or birds with prior site experience achieved faster peck-rates than immature and/or inexperienced Snow Buntings in both solitary and flock situations. Furthermore, males had higher peck-rates than females, although this advantage was only apparent in large flocks. In inexperienced birds, but not experienced individuals, residual peck-rate increased over the course of the winter. Adults (or experienced birds) and males also tended to spend more time feeding than their counterparts in early parts of feeding bouts, or in late parts of feeding bouts if the flock-size remained high.

In support of these intrinsic differences between age, sex and experience categories, I also found that some categories of Snow Buntings were more likely than others to be feeding in advantageous situations. In particular, inexperienced females were found less frequently in, and possibly avoided, large flocks. Females, especially young birds, fed less often in the early parts of the feeding bout. The likelihood of moving around the feeding station increased more with flock-size in females, but age and perhaps experience were more important indicators of retaining a feeding site at the end of a full minute's time budget. Older and more experienced birds also seemed to be better at maintaining (or possibly choosing) central positions within the feeding flock.

6.4.2 Applicability of the results

The feeding regime, although probably richer than most natural feeding patches, is unlikely to have presented Snow Buntings with an unrealistic feeding situation: they continued to feed in flocks away from the feeding station (although these were generally more dispersed and mobile), and aggressive interactions in these flocks were not infrequent, perhaps due to the clumped nature of natural feeding patches (e.g. tussocks of *Juncus squarrosus*, *J. trifidus* or surfacing cranefly *Tipula* sp. larvae). Frequent periods of ice- and snow-cover (recorded on 73% of days in the period during which time budgets for this chapter were gathered) also tended to make food sources patchy and limited in area.

My measurements of where and when an individual managed to feed also have tangible equivalents in natural situations. Natural flock-sizes varied widely and neither singletons nor flocks of a hundred or more were uncommon. Although birds tended to move as a flock in natural conditions, it was not uncommon to see the flock 'roll' gradually between foraging patches (i.e. rear birds continuously flushing over front birds to become leaders themselves, as described by Henty 1979) or for subflocks to form by groups foraging in different directions. Thus Snow Buntings would have some opportunity to choose both the size of flock in which to forage and where to feed within that flock. Leading birds might have first access to the best

patches, and age or experience might still affect how long they remained at these patches as competitors arrived. The parameters measured should therefore have been relevant to naturally encountered situations and behaviours.

Pinhead oatmeal may, however, have formed a somewhat unusual addition to the Snow Bunting diet. Unlike some seeds, it did not require complex handling or husking, merely perhaps a degree of crushing. This simplicity, however, may have *reduced* the probability of recording variation in handling efficiency between birds of differing experience.

6.4.3 Extrinsic influences on foraging success

Increases in feeding efficiency with increasing flock-size or more central position within the flock have been reported frequently in other species and this is associated with reduced vulnerability to predation (for reviews see Pulliam & Caraco 1984, Barnard & Thompson 1985). This increase may, however, be counteracted by increased social interference between birds in large flocks, especially when food sources are clumped (e.g. Goss-Custard 1977, Feare & Inglis 1979, Saino *et al.* 1994). The under-representation of time budgets from large flocks in the present study would make this latter possibility difficult to detect, although females at least seemed to be inhibited when in higher density flocks.

Several factors may have been responsible for the influence of the length of the flock's feeding bout, and the timing of a time budget within such a bout, on feeding rate. First, individuals often alighted on the surrounding fence before coming to feed on the platform, giving them time, and an elevated position, to scan for potential predators. The benefits of this pre-feeding vigilance would diminish with time into the bout, forcing birds to increase their vigilance rates whilst feeding. Second, the effect of bout-length may have been due to differences in perceived predation risk (e.g. human disturbance) between bouts, with birds taking longer to ingest a given amount of food, and hence prolonging their stay, when risk was perceived to be high. Finally, feeding priority may have dropped during the course of a bout as an individual fed. Although the short durations of feeding sessions makes it unlikely that birds would have reached satiation, they may have needed to feed quickly for only a short time to return to an appropriate energy state for the time of day (see **Chapter 8**).

The environmental and temporal variables affecting feeding efficiency played only a minor role and deserve only brief mention. Peck-rates decreased as the winter progressed, perhaps due to longer daylight hours giving birds more time to feed. In association with this, hourly rates of mass gain were lower in spring than winter (see **8.3.5**). Peck-rate increased with wind strength and with temperature. The former may be explained by birds trading increased vigilance for reduced exposure time (as in Lima 1987, but in this case to limit time spent in strong winds), while the latter may have been due to the food in the central arena becoming partly hidden by snow and ice at low temperatures, despite my efforts to keep it accessible.

6.4.4 Intrinsic influences on foraging success

There was no evidence that the magnitude of the increase in peck-rates with age and previous site experience was affected by competition: both age and previous site experience enhanced an individual's peck-rate by about 5%, whether the bird was in a flock or alone (**Fig.6.1**), and this relationship did not change in the largest flocks. The higher peck-rates of males in large flocks indicated, however, that in these situations competition could have a strong influence on feeding efficiency. These data correspond well with my observations of agonistic encounters: males won most contests over females, but interactions between age or experience categories were more even (see **7.3.3a**). The inhibitory influence of competition on feeding success would therefore have been as great for inexperienced as experienced individuals, and may even have been greater for adults.

The higher intrinsic foraging efficiency of adults was therefore probably not a result of greater agonistic ability. Instead, there may have been a difference because juveniles had not fully developed their feeding and food handling skills, although this would be surprising since delayed acquisition of skills has previously only been recognised in larger, longer-lived species with more complex feeding tasks (reviews in Burger 1988, Marchetti & Price 1989). Evidence for learning delays in passerines is limited to the first few months of life (e.g. Davies & Green 1976, Stevens 1985, Enoksson 1988) or to species taking concealed or patchy prey where the foraging task can be assumed to be difficult (e.g. Gochfeld & Burger 1984, Catterall *et al.* 1989, Jansen 1990, Desrochers 1992).

Similarly, the difference in peck-rate between experienced and inexperienced adult Snow Buntings is also unlikely to be entirely due to differences in food handling ability, because Snow Buntings quickly find and use new sources of food (Nethersole-Thompson 1966). Indeed, such an ability to adapt may be crucial to a species living at various times on the beach, farmland, or the montane zone (Lambert 1986) where unpredictable influences such as the tide, wind and snow are likely to continually upset feeding patterns. Instead, inexperienced adults may devote more time to vigilance until they have sufficient experience at the site to recognise where predators are likely to appear, and how best to avoid them. Alternatively, they may pay more attention to conspecifics until dominance relations have been resolved (e.g. Senar *et al.* 1990a).

The data on intrinsic foraging rates presented here could also be interpreted as differential mortality or emigration of birds with poorer foraging success (discussed by Desrochers 1992; inferred by Grant & Grant 1989). However, amongst individually identifiable birds for which there was a sufficient sample of observations, I found a dichotomy between birds with and without previous site experience: those without experience showed improved foraging success over the course of the winter relative to birds with experience. This suggests that birds *do* learn to forage more successfully as experience at the site increases, although disproportionate losses of less successful foragers may also contribute to the observed differences in foraging efficiency between the age and experience categories.

Male Snow Buntings, although on average larger and more dominant (see Banks *et al.* 1989, **3.3.3** & **7.3.3a**), did not have discernibly higher peck-rates than females in small flocks. However, aggression rates increased rapidly with increasing flock-size (**7.3.1**), and perhaps contributed to the poorer performance of females in the largest flocks. Large, dense flocks were a feature of days with extensive snow-cover when food was probably scarcer and more patchy. Hence intake rates may be critical at these times. The smaller body-size of females will, however, require less energy for metabolism and therefore the cost of having a lower peck-rate will depend on the rate at which the peck-rate difference increases with flock-size and the frequency with which birds feed in large flocks.

6.4.5 Variation in access to the best foraging conditions

The tendency to find fewer females feeding early in the feeding bout, for these to increase their rate of movement compared to males as flock-size increased, and for young females, at least, to be found less frequently in large flocks suggests that the intrinsic intersexual differences in foraging success would be exaggerated still further by extrinsic influences on foraging rates. Because I controlled for age and experience differences, intraspecific competition seems the most likely reason for these differences. However, skill in reacting to aggression, or familiarity with opponents, may have helped adult and/or experienced females to gain access to the bait more quickly or to benefit from feeding in larger flocks to a greater extent than younger birds. Females may also have benefitted from greater tolerance (i.e. less frequent or less intense aggression) from males. Piper (1990) found that in White-throated Sparrows smaller individuals (therefore mainly females) were more likely to share safe feeding sites with dominant heterospecific competitors than larger birds. In my study, males may have considered females to be less of a threat, or used them as a shield from more aggressive males, or perhaps females could be exploited if they came across a particularly rich source of food (discussions of coat-tail effects, The Shepherds Hypothesis and like-versus-like aggression amongst dominants in Balph *et al.* 1979, Ketterson 1979b, Rohwer & Ewald 1981, Wiley 1990, Senar *et al.* 1990a & Slotow *et al.* 1993). This could help explain why the sexes did not differ in their relative positions within flocks. It could also perhaps explain why different factors seemed to be important in enabling birds to maintain their place on the central foraging arena: females moved more as flock-size increased, but age and experience were better predictors of a bird's position at the end of the minute. Possibly females, especially older and more skilled individuals, although forced to move around the feeding platform, could return to the central arena without eliciting as much aggression as their male counterparts.

Because there was no evidence that competition within age categories affected peck-rate and time spent feeding, it is also unlikely to have been responsible for differential access to the best feeding situations. Instead, age-related experience or greater familiarity with the site or other individuals at the site, may have been responsible for the observed differences in positioning within a flock and the likelihood of being on the central arena at the end of a time budget. The greater intrinsic feeding rates of older and more

experienced Snow Buntings are therefore again likely to have been boosted by extrinsic factors affecting feeding rates.

6.4.6 Ecological implications

This chapter provides evidence that the Snow Bunting age and sex categories which are found more frequently at the high altitude sites than expected (**4.3**), are also the age and sex categories which forage most successfully there. Additionally, birds with site experience appeared to do better than naive individuals. Of course, males, adults, and experienced birds may have such an advantage at all altitudes. However, lower feeding rates may have more drastic differential consequences at high altitude sites, because snow and cold conditions will more frequently reduce foraging periods and efficiency, whilst at the same time increasing thermoregulatory demands. Hence, higher foraging rates may lower the probability that an individual will suffer a negative daily energy budget, thus increasing its ability to take advantage of the hypothesized benefits of higher altitude wintering (see **4.4**). Thus Snow Buntings may not need to compete for access to high altitude sites: individual differences in foraging efficiency may be sufficient in their own right to explain why the age and sex categories segregate between altitude bands. The influence of direct competition on site use is explored in **Chapter 7**.

Chapter 7: AGGRESSION AND DOMINANCE

7.1 INTRODUCTION

In the published avian papers which I examined for this thesis which observed some feature of behaviour and referred to it as a measure of dominance status, all but one (n=101 papers from 43 species) used the outcomes of agonistic encounters, particularly the supplanting of one bird by another, to recognize dominance. Although a few studies also included relative access to a resource as a measure of dominance, only that of Inman (1990) on captive Starlings measured dominance solely on the relative rate of access to a contested resource. The importance of aggression in establishing and maintaining dominance status is also usually acknowledged when defining dominance, e.g. Kaufmann (1983): "a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations". Most of this chapter, consistent with many other studies, broadens this definition slightly by referring to a grouping of birds as being dominant over another if, on average, its members are of superior competitive ability (i.e. are more successful in aggressive encounters) than the other (subordinate) grouping of birds.

Dominance status is often considered to be an important determinant of individual fitness and dispersal (e.g. models of Gauthreaux 1978, 1982, Pulliam & Caraco 1984, Sutherland & Parker 1985, Houston & McNamara 1988). Empirical support for this is not hard to find: apparent advantages of being behaviourally dominant are often reported in the scientific literature, whilst subordinate individuals are usually regarded as inferior (but see Rohwer & Ewald 1981).

Dominant birds may have higher survival rates than subordinates of the same species (e.g. Fretwell 1969, Baker & Fox 1978, Desrochers *et al.* 1988, Kikkawa 1980, Eden 1989, Piper & Wiley 1990b). Many factors can contribute to this. Dominants often have prior access to food (e.g. De Laet 1985, Lundberg 1985, Theimer 1987, Enoksson 1988, Choudhury & Black 1991, Ramenofsky *et al.* 1992), and can be found in the best feeding sites (e.g. Caraco 1979, Ketterson 1979a, Greig *et al.* 1985, Black & Owen 1989, Catterall *et al.* 1989, Richner 1989). Desrochers (1989) and Hogstad (1991) have shown that subordinates will use dominant birds' niches following their removal, implying that their behaviour is limited by the presence of dominant individuals.

Birds of superior competitive ability often realise advantages over subordinates in flock situations, and may be more likely to choose to forage socially (Caraco *et al.* 1989). They may achieve higher feeding rates (e.g. Feare & Inglis 1979, Baker *et al.* 1981, Goss-Custard *et al.* 1984, Piper 1990), perhaps as a result of exploiting their fellow competitors (Ens & Goss-Custard 1984, Greig *et al.* 1985, Caraco *et al.* 1989). They may also be able to feed in safer positions than other flock members (e.g. Pulliam & Millikan 1982, Schneider 1984, Hogstad 1988b, Piper 1990), which may in turn allow them to relax their vigilance levels and devote more time to feeding (Waite 1987).

Greater access to food, or safety from predators, may explain why dominants are often heavier than subordinates (Kikkawa 1980, Piper & Wiley 1990b, Muma & Weatherhead 1991; but see also Ekman & Lilliendahl 1993). Dominants have also been shown to deposit fat reserves more quickly (Weidenmann & Rabenold 1987, Lindstrom *et al.* 1990), lose body-mass less rapidly in bad conditions (Wagner & Gauthreaux 1990) and show less signs of nutritional stress (Grubb 1989). Dominants are also less quick than subordinates to return to food sources after disturbance from a predator (e.g. De Laet 1985, Hogstad 1988c). This infers that the latter are more willing to take risks, perhaps because they place greater value on the increase in foraging time.

Dominants may also have smaller ranges (Metcalfe 1986, Piper & Wiley 1990a) and exhibit greater site tenacity (Terrill 1987). Subordinate individuals of migrant species often have to suffer longer movements to wintering grounds, and a consequent reduced survival rate (see Gauthreaux 1978, Ketterson & Nolan 1982).

Superior competitive ability may ultimately lead to increased fecundity, even in territorial species. This may result from access to better territories (e.g. Smith 1976, Moller 1988, Eden 1989, Post 1992) or mates (Smith 1976, Moller 1988, Ekman 1990, Post 1992).

In some circumstances, because aggression also involves costs and risks (Huntingford & Turner 1987), dominant birds might defer to subordinates because the reward of winning may be relatively trivial for the former (e.g. more food when nearly satiated), but not the latter (some food when previously deprived). Moreover, Senar *et al.* (1989, 1990a) suggest that flock cohesion in wintering Siskins may be promoted by dominance reversals. Not surprisingly, the nature and characteristics of contests won by subordinates over dominants can differ from those won by dominants over subordinates (Senar *et al.* 1989). Therefore consideration of contest characteristics (such as the tendency to initiate contests, the likelihood of retaliation, or the degree of contest escalation) should underpin dominance relationships. Dominants, for example, should win contests more easily than subordinates (i.e. with less need to escalate) when pursuing a given role in a contest. Moreover, variation in encounter traits can tell us more about the relative importance of winning to different groups of individuals under contrasting conditions (e.g. Yasukawa & Bick 1983, Popp 1987a,b, Nilsson 1989, Senar *et al.* 1989, 1992b, Wilson 1994).

In this chapter I look at the circumstances under which Snow Buntings became involved in aggressive interactions, and the proximate consequences of their aggression. I also describe the characteristics of agonistic contests in some detail, to show how victories were achieved. However, the most important part of the chapter is devoted to establishing whether or not stable differences in dominance status exist among different types of Snow Buntings. Many factors have been shown to affect dominance status, although the importance of each varies between studies. Age, sex, size and prior residence are the most frequent correlates of dominance in birds (reviewed by Gauthreaux 1978). Their relative roles and influences on

aggression and dominance amongst Snow Buntings are presented below.

7.2 METHODS

7.2.1 Definition of a contest

Throughout this chapter, an aggressive interaction, encounter or contest between two Snow Buntings is defined as occurring if the approach of one bird appeared to cause the withdrawal of the other, or alternatively the approach of the first was rebuffed by the second. Priority of access to a resource, or avoidance behaviour (e.g. Oberski & Wilson 1991), although perhaps also indicative of dominance or submission, were not recorded in this study. The vast majority of aggressive interactions occurred whilst birds were feeding, but occasional contests appeared to be stimulated by access to loafing sites, prominent perches (posts and boulders used prior to feeding bouts) or pools of water used during spells of drinking or bathing.

Over 12,000 aggressive interactions were observed during this study (**Table 7.1**), and the following data were recorded:

a) The identity of the Winner and Loser of the contest, or the age and sex of unringed birds (see **6.2** for accuracy of age/sex assessment in the field). The Winner was judged to be the bird in possession of the contested resource at the end of the encounter. In a small proportion of contests (1.1%), either both birds retained access to the contested resource, or both birds retreated. These contests were treated as draws.

b) The type of contest, a measure of its escalation. I defined Threats as contests where there appeared to be no physical contact between the contestants. In contrast, Fights occurred if one or both contestants appeared to peck the other, perhaps on several occasions. These were further divided for some analyses into Short and Long Fights. The latter were distinguished because they commonly lasted for several (3+) seconds and involved repeated attacks and retaliations from both contestants. Long Fights were usually characterised by greater movement and wing-flapping of the two birds, and often they pushed against each other chest-to-chest with raised head and neck.

c) The Attacker was defined as the bird which initiated the contest. This usually involved a lunge at the Target bird, or a close-range 'stare' with open beak.

d) The Possessor was the individual which had access to the contested resource at the beginning of the contest, while the opponent was termed the Intruder. In some contests the Winner attacked the Loser but returned at the end of the encounter to its original position. In these cases the contested resource may have been individual space and the Winner was assumed to be the Possessor.

In some situations, especially if many birds were feeding simultaneously at a small food patch, aggressive encounters happened too frequently for all of the above information to be recorded. At these times,

emphasis was put on identifying the Winner, Loser and type of as many contests as possible.

Table 7.1. Summary of frequency and characteristics of data recorded during aggressive interactions amongst Snow Buntings in winters 1988/89 to 1992/93. *In 1988/89 only the outcomes of contests between individually marked birds were recorded. For definitions see text.*

	1988/89	1989/90	1990/91	1991/92	1992/93	Σ
No. of encounters:	1157	2276	2879	2330	3367	12009
% of encounters drawn:	0.5	1.6	1.3	0.9	0.9	1.1
% Attacker noted:	0	37	42	79	86	57
% Possessor noted:	0	36	41	79	86	56
% type noted:	0	95	99	98	100	89
% age/sex of both birds noted:	96	91	99	97	82	91
% both birds individually identifiable:	100	58	68	56	49	61
No. of individually ringed birds involved in encounters:	114	188	115	106	63	
Mean no. of encounters per ringed bird:	20	18	41	32	74	
Median no. of encounters per ringed bird:	14	8	13	21	56	
Interquartile range:	5-29	2-24	3-47	6-39	10-121	
% of encounters involving at least one adult male:	57	71	95	79	84	80

Contests between the same two individuals were usually separated by several seconds or longer in which both birds resumed some behaviour other than aggression. It was possible, however, for an individual to be involved in one contest, then, in the ensuing movement and confusion, to be forced immediately into a second or even third contest with further birds. In this respect, contests were probably clumped, rather than randomly distributed in time.

7.2.2 Sources of data

Throughout winters 1988/89 to 1992/93 the characteristics and outcome of aggressive interactions were recorded at all sites on Cairn Gorm whenever contests were seen. If no other field manipulation of the birds was under way (e.g. trapping, feeding time budgets, attraction to weighing balances, etc.) this aspect of fieldwork was given high priority. It was often possible, for example, to increase the rate of interactions by providing only a small patch of artificial food (see **7.3.1b**).

Additionally, data on rates of aggression were collected from situations where more control over environmental parameters, notably the amount of food provided and the area over which it was scattered, was possible.

Firstly, during the 1989/90 winter Snow Buntings were attracted to a small artificial feeding arena at CIFS. Individuals were observed for up to a minute during which time I measured time use, feeding rates and other behavioural and spatial parameters (details in **6.2**). The main purpose of these time budgets (referred to throughout this chapter as feeding budgets) was to look at the factors affecting feeding rates, but since the number of aggressive interactions was also noted, they were also the largest available data set during the study period in which to look for factors affecting aggression. The size of the arena (0.5m by 0.6m) was constant throughout this observation period.

Secondly, in February and March 1992, I tested whether reduction in patch-size, rather than the amount of food available, caused greater aggression rates in Snow Buntings by varying the area over which a constant amount of artificial food was spread. This simulated the reduction in foraging areas which would occur naturally as a result of snowfalls, although the amount of available food would also decrease at such times. A metre-square was demarkated with pebbles, and roughly 80g of peanut granules was either scattered throughout the square or concentrated in a 20cm x 20cm patch in the middle of the square. Only one patch-size was available at a site (PTB, CCTB or CCPB) at any one time while observations were being made, although on some days single patches were available at two sites on Cairn Gorm. I attempted to provide patches of a different size on alternate days, but, if all the food had not been eaten since the last visit, this was not possible. I recorded time budgets, subsequently referred to as patch budgets, of up to 30s duration, depending on how long the focal bird remained in the metre square. Subjects were chosen at random (as in **6.2.1**), although colour-ringed birds were picked in preference to unringed individuals.

Feeding parameters were not noted, although only birds whose main activity was feeding were included in the analysis. All aggressive interactions and their characteristics were noted, along with the identity of the focal individual, the time from the start of the flock's feeding bout, and the flock-size at the start and end of the patch budget, using definitions similar to those outlined in **6.2.**

Finally, I gathered data on the consequences of aggression by attracting flocks of Snow Buntings to a 0.6m by 0.6m patch of oatmeal at CIFS during late February/early March 1993. The birds were video-taped as they fed, and during the commentary as many birds as possible were identified. The patch was positioned centrally in relation to the area visible on the video-film, which was approximately 1.2m wide at the feeding patch. For each aggressive interaction where one or both of the contestants was identified, I recorded: (a) the Winner and Loser, (b) whether the contest began On the patch or outside it (Off), (c) the type of contest, (d) the locations of the Winners and Losers 5s after the contest was over (On the patch, Off the patch, or out of view), and (e) whether or not the Winners and Losers pecked at food during the 5s following the end of the contest.

7.2.3 Comparisons of dominance status

The ideal method of studying dominance relationships is to construct a winner-loser matrix (as in Brown 1975). This method ranks the competitors in a matrix from top to bottom, minimising the number of losses occurring below the diagonal. However, the matrix method was mostly impractical in my study because of the large number of individuals present and their high turnover rate during the winter. I have only used it to test whether the linear relationship seen amongst the most frequently recorded birds was a result of true differences in each individual's ability to win contests, or simply due to chance (see **7.3.3b**; Appleby 1983). Nor was it desirable to use just the proportion of encounters won, or the proportion of other birds beaten, because of the possibility that contests were not randomly distributed amongst age, sex or experience categories. Instead, I compared the proportion of interactions or dyads (all interactions between two individuals) won between age/sex categories in order to determine dominance. Where possible, this was taken to the individual level by looking at the proportion of interactions or dyads that a particular individual won against other age/sex categories. Further details are provided in **7.3.**

7.3 RESULTS

7.3.1 Factors affecting the rate of aggressive interactions

7.3.1a Results from feeding budgets

To quantify the environmental and individual factors affecting the likelihood of an aggressive interaction (AGGRESSION) occurring during a feeding budget, I firstly selected the 1177 feeding budgets at CIFS

where more than one bird was present, the feeding budget lasted a full 60s, the focal bird remained on the arena at the end of the minute, and the flock-size at the end of the feeding budget did not differ from that at the start of the budget by more than a factor of four (see **6.2.1** & **Table 6.1** for further details).

Because singletons were not considered, I categorised FLOCK-SIZE (average of values at start and end of the time budget) slightly differently to the categories described in **6.2.1**: Small flocks consisted of 1.5-2.5 individuals (n=554), Medium flocks had 3-6 birds (n=458) and Large flocks had at least 6.5 birds (n=165). These categories were chosen to increase the minimum number of birds considered to be a Large flock without compromising sample size. Feeding budgets were categorised as Early or Late if the time elapsed between the start of the flock's feeding bout and the start of the focal bird's feeding budget (TIME FROM START) was less than or more than two minutes respectively (as in **6.2.1**). AGE, SEX and EXPERIENCE of focal birds were calculated as in **Chapter 6**. I also looked for effects of weather variables (see **2.3**), but recategorised them as follows:

a) 9AM TEMPERATURE: 0 = at or below freezing; 1 = above freezing but below 5°C; 2 = at or above 5°C.
b) SNOW COVER: 0=ground not ice or snow covered; 1=ground covered partly or completely by ice and/or snow.
c) SNOW DEPTH: 0 if no snow; 1 if 1-9cm of snow; 2 if 10cm snow or more.
d) WIND SPEED: 0 for average wind speeds below 40mph; 1 if 40mph or more.

The likelihood that the focal individual would be involved in an aggressive interaction was significantly higher in Large than Medium or Small Flocks (**Fig.7.1**; loglinear test for the interaction between AGGRESSION and FLOCK-SIZE: $X^2_2=107.5$, $P<0.001$), and this result was independent of any other significant interactions included in models with a third variable (**Table 7.2**). The likelihood of being involved in aggression was not influenced by TIME FROM START, AGE, SEX, EXPERIENCE or WIND SPEED, but was associated with cold, snowy conditions (**Table 7.2**). Involvement in aggression was particularly frequent when temperatures were below freezing (**Fig.7.1**).

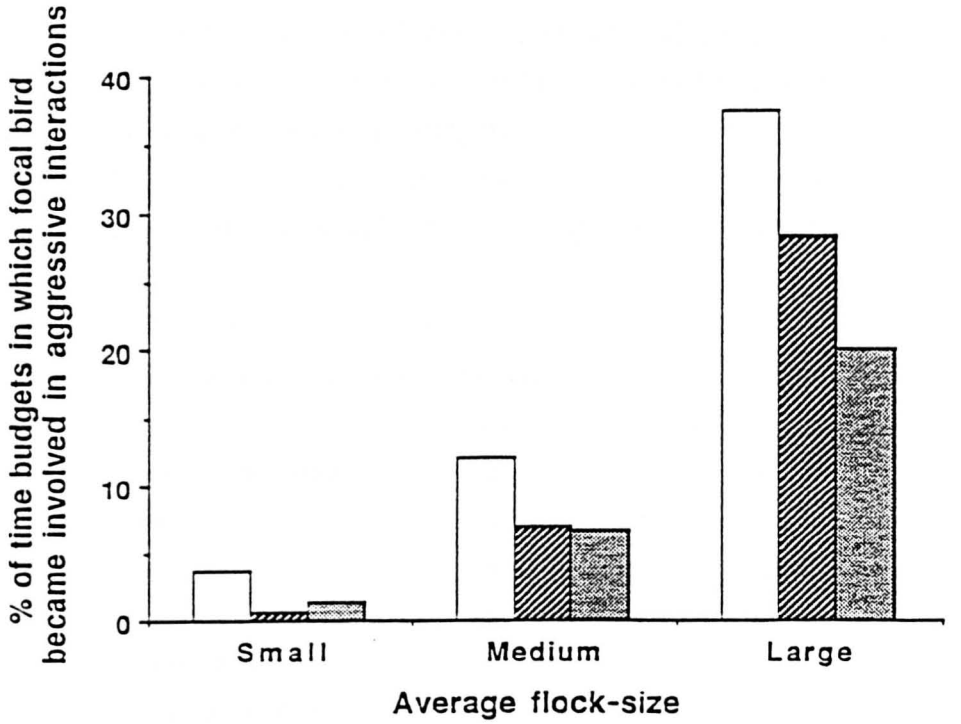


Fig.7.1. The likelihood that a Snow Bunting would be involved in an aggressive interaction in its one minute feeding budget, in relation to the average flock-size (Small = 1.5-2.5 birds, Medium = 3-6 birds, and Large = 6.5+ birds) and 9a.m. temperature (blank bars represent temperatures ≤ 0°C, hatched bars = 1-5°C, stippled bars ≥ 6°C). *Sample sizes are (left to right) 132, 281, 141, 131, 226, 103, 40, 95 & 30 feeding budgets.*

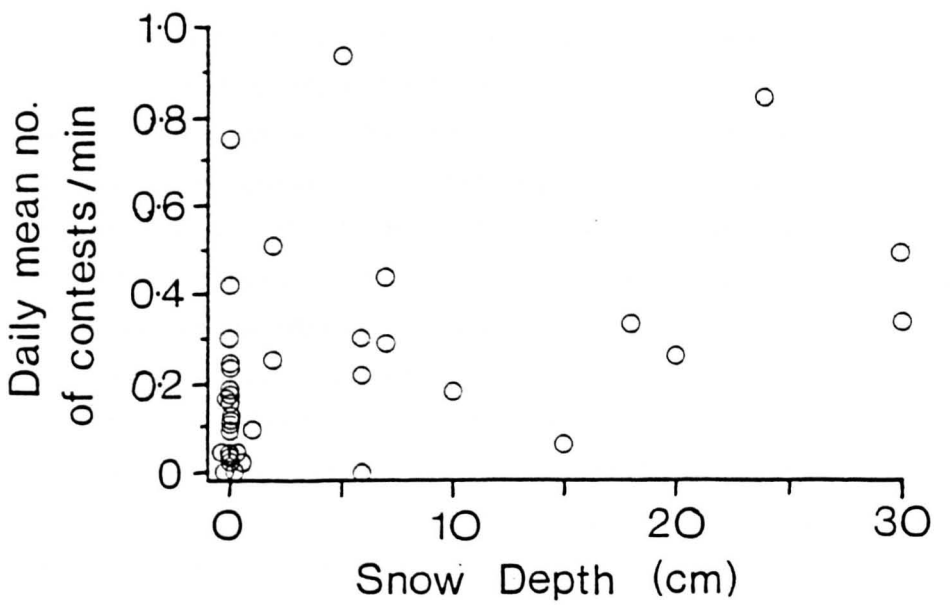


Fig.7.2. The relationship between the daily mean rate of aggression in Snow Bunting feeding budgets and snow depth. *r_s=0.49, n=36 days, P=0.002.*

Table 7.2. Loglinear analysis of the effect of independent variables on the probability that a focal Snow Bunting would take part in an aggressive interaction during its one minute feeding budget. *As well as involvement in aggression (AGGRESSION) and the independent variable, FLOCK-SIZE was also used as an explanatory variable in all models, but none of the 3-way interactions approached significance.*

Independent Variable	Chi-square	d.f.	Probability
TIME FROM START	1.58	1	0.21
SEX	1.21	1	0.27
AGE	0.52	1	0.47
EXPERIENCE	1.36	1	0.24
WIND SPEED	0.01	1	0.92
9AM TEMPERATURE	8.19	2	0.017
SNOW COVER	2.65	1	0.10
SNOW DEPTH	5.33	2	0.07

It is possible that rates of aggression were high only on particular days and that a large number of time budgets from some of these days may have caused a spurious relationship with weather conditions. Additionally, in some feeding budgets it appeared that birds left the feeding platform as a result of involvement in aggression (see also **7.3.2**). My selection of budgets may therefore have been biased towards those with low rates of aggression. To test these possibilities I calculated, on a daily basis, the total duration of feeding budgets and the total number of aggressive interactions recorded during these budgets and hence calculated a daily mean aggression rate. The limitations on the inclusion of time budgets were similar to the previous analysis, but shorter budgets were also included. For each day I calculated a mean flock-size (employing the log10 values of FLOCK-SIZE from each included feeding budget) and used SNOW DEPTH, 9AM TEMPERATURE and WIND SPEED as weather variables (actual values as detailed in **2.3**). Only days on which there were more than ten valid feeding budgets were included (n=36 days). The daily mean aggression rate was higher on days with greater snow-lie (**Fig.7.2**), lower temperatures and larger flocks but was not influenced by wind speed (**Table 7.3**), supporting the results of the previous paragraph.

Table 7.3. Spearman rank correlation coefficients between daily mean rate of aggression in focal Snow Buntings, mean flock-size and weather variables.

Variable	r_s	P
Mean flock-size	0.38	0.022
SNOW DEPTH	0.49	0.002
9AM TEMPERATURE	-0.37	0.025
WIND SPEED	0.10	0.56

7.3.1b Results from patch budgets

The patch budgets recorded in February and March 1992 were mainly designed to find out whether rates of aggression increased as patch size was reduced. Additionally, however, because feeding variables were not recorded, it was possible to record more details of each aggressive encounter, notably the type of interaction (see **7.3.5e**), and whether the focal bird was an Attacker or a Target.

In total, 200 patch budgets were recorded from small ($0.04m^2$) patches and 182 from large ($1.0m^2$) patches. FLOCK-SIZE was again categorised as in the previous analysis but as few feeding bouts lasted for more than two minutes, the relative timing of the patch budget (TIME FROM START) was categorised as Early if less than one minute elapsed between the start of the flock's feeding bout and the start of the focal individual's patch budget, and Late if this time was one minute or more. Again, because interactions were not always independent events, I recorded aggression as whether or not an interaction occurred during the patch budget (if not, AGGRESSION=0; otherwise AGGRESSION=1), rather than the number of aggressive interactions occurring in a patch budget. Similarly, I defined two variables ATTACK and TARGET according to whether or not the focal bird was an Attacker or a Target, respectively, during its patch budget. It was, of course, possible for a bird to be neither or both. I then looked for an influence of age and sex on whether a bird got involved in an aggressive interaction, but also considered whether different age/sex categories were more likely to be Attackers or Targets.

The likelihood of involvement in aggression was significantly and independently related to flock-size, patch size and time from the start of the flock's feeding bout (loglinear analysis with the four variables AGGRESSION, FLOCK-SIZE, PATCH-SIZE and TIME FROM START: AGGRESSION*FLOCK-SIZE,

X^2_2=53.9, P<0.001; AGGRESSION*PATCH-SIZE, X^2_1=35.1, P<0.001; AGGRESSION*TIME FROM START, X^2_1=11.5, P=0.003; there were no significant higher order interactions). The likelihood of involvement in aggression was higher in larger flocks and in smaller patches (**Fig.7.3**). It was apparently also greater in the Early parts of a feeding bout, but as there was no significant relationship between aggression and time from the start of the flock's feeding bout in the larger sample of feeding budgets (**7.3.1a**) I examined this result further by looking at the effect of TIME FROM START *within* patch sizes and also *within* flock-sizes.

After controlling for flock-size, the focal bird was more likely to be involved in aggression Early in the time budget if the patch was small, but not if the patch was large (**Fig.7.3**; small patch: loglinear X^2_1=7.20, P=0.007; large patch: X^2_1=0.16, P=0.68). Birds were also more likely to interact Early than Late in the time budget in small flocks and to some extent in medium flocks, but the likelihood of involvement in aggression remained high throughout the feeding bout in large flocks (**Fig.7.3**; small flock: loglinear X^2_1=4.39, P=0.036; medium flock: X^2_1=3.56, P=0.06; large flock: X^2_1=0.29, P=0.59).

Did the age and sex of the focal bird affect its chances of becoming involved in aggression? I examined this by including AGGRESSION, the four age/sex categories, PATCH-SIZE and FLOCK-SIZE in a loglinear model. To simplify the model, PATCH-SIZE and FLOCK-SIZE were included as one treatment variable with six possible categories: small patch & small flock, small patch & medium flock, etc. None of the age/sex categories were significantly more or less likely to become involved in aggression during their patch budgets (**Fig.7.4**; AGGRESSION*AGESEX, loglinear: X^2_3=1.08, P=0.78). However, this analysis does not differentiate between whether birds *willingly* got involved in aggression (i.e. initiated an encounter) or were forced to get involved when other birds targeted them. Therefore I repeated the previous analysis after substituting AGGRESSION by ATTACK and by TARGET.

There was a significant age/sex influence on whether the focal bird attacked another individual during its patch budget: adult females were less likely to attack than the other age/sex categories (**Fig.7.5**; ATTACK*AGESEX: loglinear X^2_3=8.03, P=0.045). Although the probability of being targeted did not differ significantly between the age/sex categories (TARGET*AGESEX: loglinear X^2_3=3.30, P=0.35) the direction of the differences emphasised the impression that juvenile males tended to initiate aggression and adult females were more frequently targets, whilst adult males and juvenile females were as likely to attack as be attacked (**Fig.7.5**).

7.3.2 The consequences of aggression

The behaviours and subsequent locations of both contestants in 719 aggressive interactions were recorded with a video camera in February/March 1993. Many contestants were not aged because the resolution of the video film was often only sufficient to tell males from females; hence some analyses were performed using

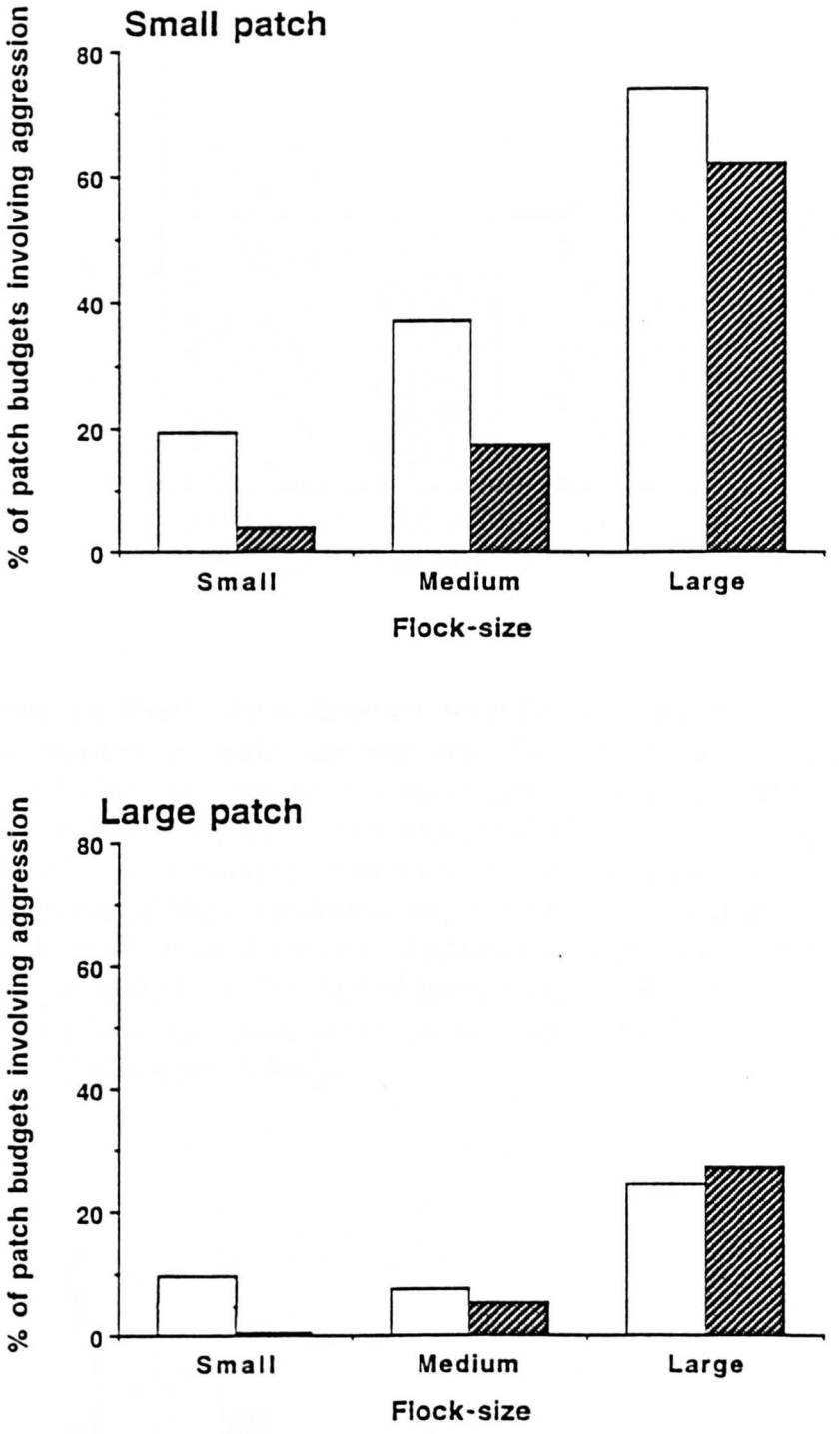


Fig.7.3. The likelihood of involvement in aggression during a Snow Bunting patch budget in relation to flock-size and time from the start of the flock's feeding bout, in small patches (above) and large patches (below). *Blank bars represent Early patch budgets and hatched bars Late patch budgets. Sample sizes for the small patch are (left to right) 41, 25, 43, 34, 27 & 29 patch budgets; for the large patch they are 52, 12, 40, 19, 37 & 22 patch budgets. Patch-size, flock-size and time into the feeding bout had independent significant effects on aggression rates (see text).*

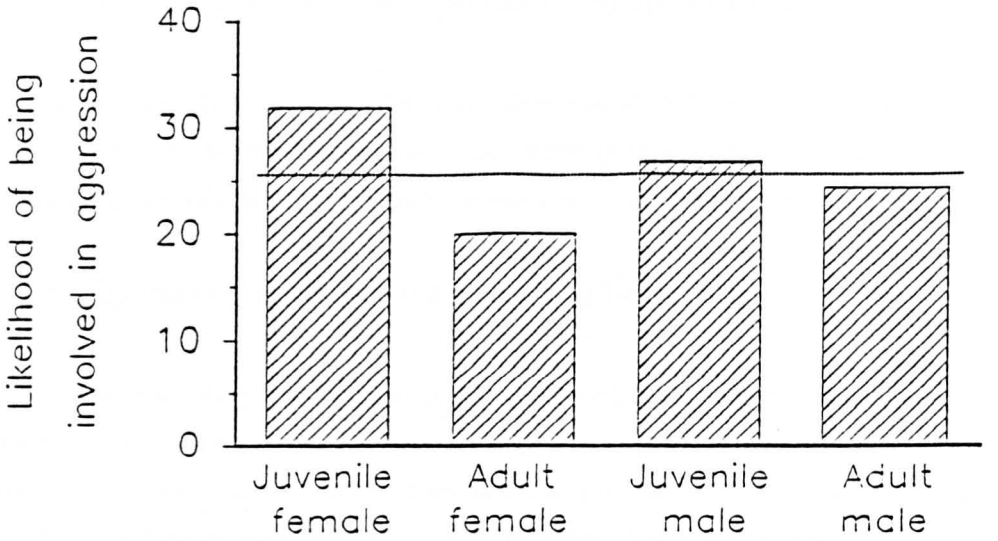


Fig.7.4. The relative frequency with which focal Snow Buntings became involved in aggression in relation to their age and sex. *The likelihood of being involved in aggression varied widely amongst six treatments (patch-size & flock-size categories - see text) so, for illustrative purposes, I calculated the deviation in percentage frequency of aggression of each age/sex category from the overall mean for each of its six treatments. I then took the mean of these six deviations for each age/sex category, and added or subtracted this from the mean percentage frequency of aggression across all treatments to obtain the height of the bars. The dashed bar represents this mean percentage of patch budgets which involved aggression across all treatments, i.e. 26%. Sample sizes left to right are 53, 72, 72 & 184 patch budgets.*

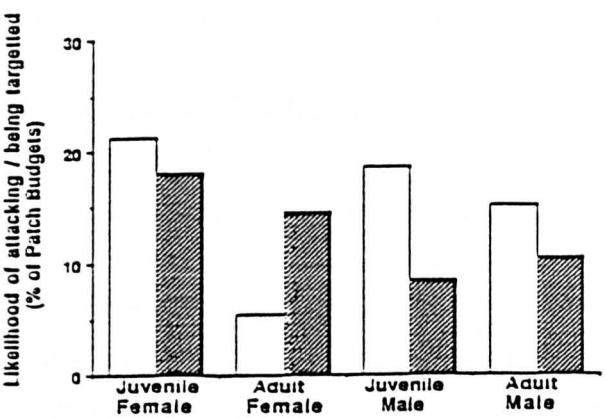


Fig.7.5. The relative frequency with which focal Snow Buntings were Attackers (blank bars) or were Targets (hatched bars) during patch budgets, in relation to their age and sex. *The height of the bars was calculated using a similar method to that outlined in Fig.7.4. Sample sizes for each bar are also as given in Fig.7.4.*

AGE, SEX and EXPERIENCE categories in preference to the four age/sex groups.

I compared the contestants' locations after 5s and their probability of pecking within 5s, and looked for variation associated with the initial location of the contest (a control variable of otherwise little relevant importance), the type of contest, and the age, sex and experience of the contestant.

7.3.2a Influence of aggression on feeding behaviour

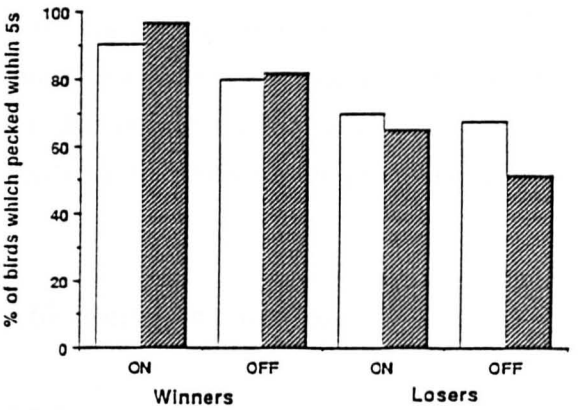
Was the Winner more likely than the Loser to resume feeding quickly after the end of a contest? As all the observations were made pairwise between Winners and Losers, an overall comparison between the frequency of pecking within 5s of the interaction was possible without controlling for other factors. Overall, 88% of Winners were able to peck at food within 5s of the encounter, but only 68% of losers (X^2_1=88.6, P<0.001). This difference was apparent whether the encounter took place On or Off the feeding patch (On: 92% vs 69%, X^2_1=81.4, P<0.001; Off: 81% vs 65%, X^2_1=12.7, P<0.001). As expected, Winners were more likely to feed within 5s if they were On the patch than Off it (X^2_1=17.2, P<0.001) but, although Losers showed the same pattern, the magnitude of the difference was not significant (X^2_1=1.03, P=0.32). The type (degree of escalation) of encounter did not seem to alter the probability of feeding: all four comparisons within outcome and location categories were insignificant and there was no obvious common pattern between the four tests (**Fig.7.6**).

There was no suggestion that age or experience affected the probability that a bird would be able to peck within 5s of an interaction (minimum P from the four chi-square tests performed within outcome and location categories was 0.30 for AGE, and 0.24 for EXPERIENCE). However, females were more likely than males to peck within 5s if they lost an encounter, irrespective of location (**Fig.7.7**; On patch: X^2_1=6.12, P=0.015; Off patch: X^2_1=5.29, P=0.021). No difference between the sexes was apparent if the bird was a Winner (**Fig.7.7**; both On and Off patch: X^2_1=0.0, P>0.95).

7.3.2b Effect of aggression on feeding location

In total, 72% of birds that won encounters, but only 42% of Losers, were still On the patch 5s later; 9% of Losers compared to 3% of Winners had flushed completely from the site within 5s (X^2_2=135.5, P<0.001). Irrespective of outcome, more birds were likely to be On the patch after 5s (and fewer to have flushed completely) if the contest took place On the patch as opposed to Off it (**Fig.7.8**; for Winners X^2_2=56.8, P<0.001; for Losers, X^2_2=18.0, P<0.001). Again, there was no significant difference in future location of birds in relation to the degree of escalation of the interaction within the four outcome and location categories (P's=0.08, 0.25, 0.25 & 0.45).

Fig.7.6. The percentage of Snow Buntings which pecked at food within 5s of the end of an interaction, in relation to whether they Won or Lost the interaction, whether the interaction took place On or Off the patch of food and the type of contest (Threats are represented by open bars, Fights by hatched bars). *Sample sizes (left to right) are 412, 92, 176 & 39 interactions for both Winners and Losers.*



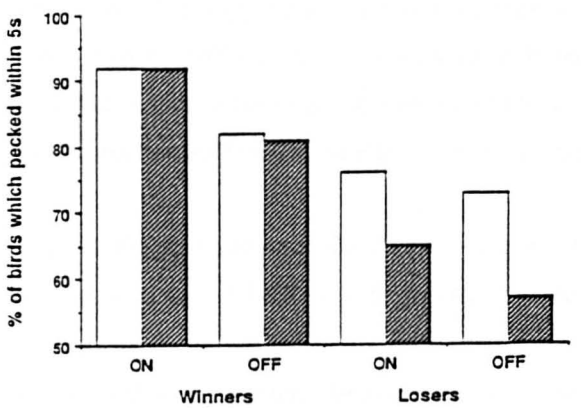
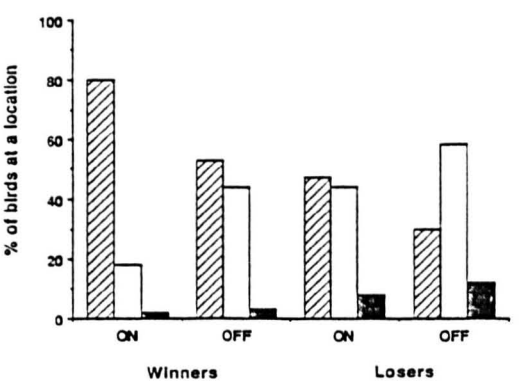


Fig.7.7. The percentage of Snow Buntings which pecked within 5s of the end of an interaction in relation to whether they Won or Lost the interaction, whether the interaction took place On or Off the patch of food and the contestant's sex (females are represented by open bars, males by hatched bars). *Sample sizes (left to right) are 72, 421, 28, 185, 196, 289, 96 & 113 interactions.*

Fig.7.8. The location of a Snow Bunting 5s after it was involved in an interaction in relation to whether it Won or Lost the interaction and whether the interaction took place On or Off the patch of food. *Hatched bars represent birds On the patch after the encounter, blank bars those Off the patch but visible, and stippled bars those which had flushed completely. Sample sizes of the four groups (left to right) are 504, 215, 504 & 215 interactions.*



I also tested for differences between males and females, adults and juveniles, and naive versus experienced birds amongst the four outcome and location categories. Two of the twelve tests reached significance: for fights On the patch, naive Winners were more likely than experienced Winners to remain On the patch (X^2_1=5.59, P=0.018) and young Losers were more likely to remain On the patch than adult Losers (X^2_1=4.35, P=0.04).

7.3.3 Factors affecting individual differences in dominance

7.3.3a The role of sex, age and experience.

The overall outcome of contests between birds of known age and sex was consistent between winters and highly significant across all winters for all pairwise age/sex comparisons (**Table 7.4**). Within age categories, males won approximately 90% of encounters with females. Within sexes, juveniles won a greater share of contests against adults than expected, but the difference was slightly less one-sided: juvenile males won 69% of their contests with adult males, and juvenile females 60% of contests with adult females. Neither the percentages of contests won by juvenile males against adult males, nor the percentage won by males against females, changed over the course of the winter (**Table 7.5**).

To examine the possibility that these results, particularly within sex categories, were due to a small number of birds which interacted far more frequently than the average bird, I grouped all interactions into dyads (i.e. every two birds that interacted with each other), the data for each winter being kept separate. The winner of a dyadic encounter between two birds was simply the individual which won most of the encounters between them, even if there was only one contest between the pair (62% of dyads involved single encounters, 96% were based on five encounters or less). Again patterns were very similar between years, and overall the percentage of dyadic encounters won by an age/sex category against any other was very similar to the percentage of individual encounters won: males won 87% of all dyadic encounters with females, and juvenile males and females won 70% and 61% of dyads within sexes (**Table 7.6**).

Table 7.4. The annual percentage of interactions won in contests between each of the four age/sex categories of Snow Buntings. *The percentage given is the percentage of interactions won by the first named age/sex category. The number of contests is given in brackets. The significance level is that associated with a chi-square test under the null hypothesis that the two age/sex categories should win an equal number of contests.*

	1988/89	1989/90	1990/91	1991/92	1992/93	Σ
Adult male	24	40	41	26	21	31
vs	(348)	(469)	(359)	(454)	(418)	(2165)
Juvenile male	***	***	***	***	***	***
Adult male	89	92	82	87	85	86
vs	(130)	(378)	(492)	(282)	(515)	(1797)
Adult female	***	***	***	***	***	***
Adult male	57	82	94	77	67	76
vs	(30)	(132)	(31)	(286)	(87)	(566)
Juvenile female		***	***	***	**	***
Juvenile male	92	95	91	92	90	92
vs	(146)	(140)	(58)	(89)	(134)	(567)
Adult female	***	***	***	***	***	***
Juvenile male	91	95	100	85	93	90
vs	(57)	(63)	(8)	(104)	(55)	(287)
Juvenile female	***	***		***	***	***
Adult female	36	52	25	35	39	40
vs	(22)	(62)	(4)	(94)	(49)	(231)
Juvenile female				**		**

*** P<0.001, ** P<0.01, * P<0.05

Table 7.5. The relationship between the percentage of contests won by Snow Bunting age/sex categories and winter date. *Date was measured in consecutive half months from November until March, but only half-months with more than 50 relevant contests were included. n is the sample size of half-months. Neither the percentage of contests won by juvenile males (vs adult males) nor males (vs females) changed significantly over the course of the winter.*

Contestants	% wins in a half-month period: Minimum	Maximum	n	r_s	P
Juvenile male vs adult male	59	73	8	-0.26	0.53
Male vs female	81	95	9	0.33	0.38

Table 7.6. The percentage of dyadic encounters won in contests between each of the four age/sex categories of Snow Buntings. *The percentage given is the percentage of dyadic encounters won by the first named age/sex category. Dyads were calculated on an annual basis: thus pairs of birds which interacted in more than one winter would contibute more than one dyad. Drawn dyads (only 3.4% of all dyads) were allocated equally to each age/sex category. The significance level is that associated with a chi-square test under the null hypothesis that both age/sex categories should win an equal number of dyads.*

	% Dyads Won	n	X^2_1	P
Adult male vs Juvenile male	30.1	657	102.9	***
Adult male vs Adult female	87.3	558	308.6	***
Adult male vs Juvenile female	76.5	147	40.3	***
Juvenile male vs Adult female	93.9	198	151.2	***
Juvenile male vs Juvenile female	88.1	80	45.0	***
Adult female vs Juvenile female	39.0	50	2.0	n.s.
All males vs All Females	86.8	1000	538.8	***

*** P<0.001, ** P<0.01, * P<0.05

The large sample of interactions recorded (**Table 7.1**) allowed me to define three levels of prior site experience in this analysis. Unringed birds were considered to have least prior site experience because on average they had probably been on Cairn Gorm for only a short period of time (see **6.2**). Ringed birds which had been trapped on Cairn Gorm for the first time during the winter when the observation took place were considered to have intermediate site experience, while those ringed in a winter previous to this had most prior site experience (no attempt was made to control for the number of times a bird was seen in previous winters because few birds which visited Cairn Gorm transiently returned in future winters - **Fig.9.3**). By definition, ringed juveniles could only have intermediate levels of site experience, but a comparison with unringed juveniles was still possible.

Because the differences between the age/sex categories were substantial, I tested for differences in dominance between the experience categories *within* each age/sex category (**Table 7.7**). The percentage of encounters won by unringed birds was greater than that of present-year ringed birds in 14 of the 16 age/sex pair comparisons (Wilcoxon matched pairs test: $z=3.21$, $P=0.001$), and five of these comparisons were significant in their own right. Amongst adults, the percentage of encounters won by present-year ringed birds was significantly greater than that won by previous-year ringed birds in half of the eight age/sex pair comparisons, and three other tests were in the same direction (overall Wilcoxon matched pairs test: $z=2.24$, $P=0.025$). Overall, it can be concluded that birds with *less* site experience were more likely to win encounters against birds of a particular age/sex category than were birds with *more* site experience. The differences between experience categories were less pronounced (2-14%, **Fig.7.9**) than those between age/sex categories, and did little to alter the overall effect of age and sex on the outcome of encounters between age/sex categories (**Table 7.7**).

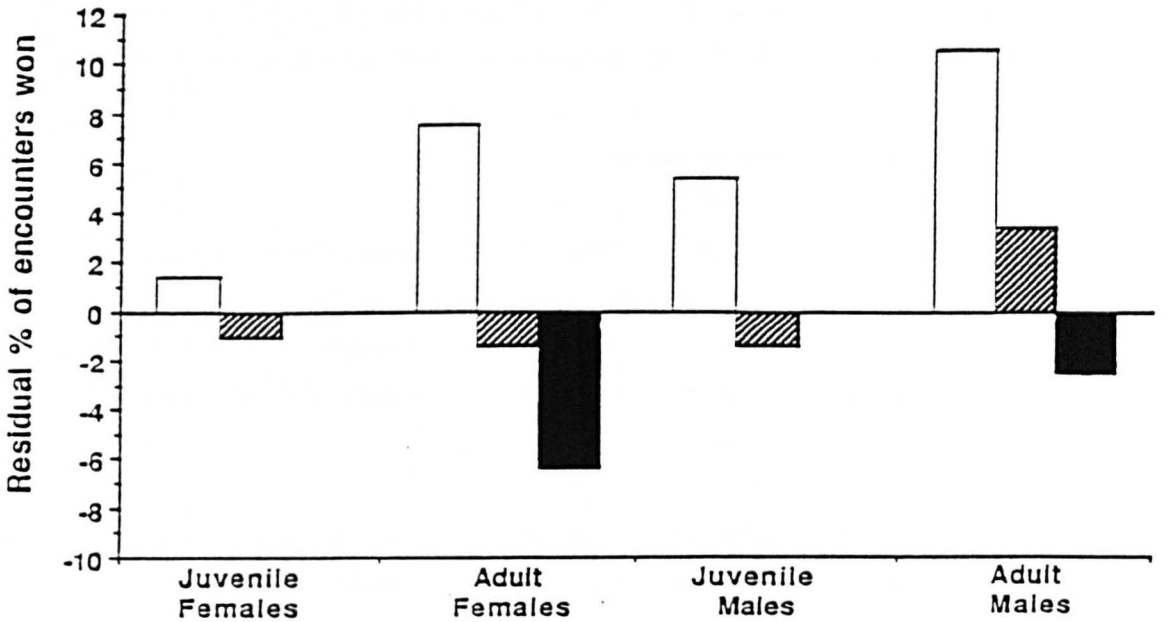


Fig.7.9. The effect of experience on the percentage of encounters won by each of the four age/sex categories of Snow Buntings. *The residual percentage of encounters won is derived for illustrative purposes from the average difference of each experience class from the mean against the four age/sex categories of opponent. Unringed birds (least experienced) are depicted by open bars, present-year ringed birds (intermediate experience) by hatched bars, and previous-year ringed birds (most experienced, but not applicable to juveniles) by stippled bars. The percentage of encounters won decreased with experience (see text and* ***Table 7.7*** *for statistical analysis).*

Table 7.7. The percentage of contests won in relation to experience category for all known age/sex category pairings of Snow Buntings. *Present WR and Previous WR indicate birds which were ringed in the winter when the aggression was noted (intermediate experience) or before that winter (most experienced) respectively. Unringed birds had least site experience by definition. The probability given below each age/sex category pairing is that associated with a chi-square test under the null hypothesis that all experience categories should win an equal number of contests (1 d.f. for comparisons within juvenile age/sex categories, 2 d.f. for comparisons within adults).*

	Age/sex category of opponent:			
Prior Site Experience	Juv. Female	Juv. Male	Ad. Female	Ad. Male
Unringed Juv. Female	54 (83)	12 (105)	60 (131)	22 (306)
Present WR Juv. Female	47 (117)	8 (182)	59 (100)	25 (258)
	n.s.	n.s.	n.s.	n.s.
Unringed Juv. Male	97 (61)	61 (172)	92 (146)	73 (575)
Present WR Juv. Male	88 (226)	48 (841)	92 (420)	68 (1585)
	n.s.	**	n.s.	*
Unringed Ad. Female	51 (89)	12 (172)	64 (200)	16 (616)
Present WR Ad. Female	34 (53)	10 (177)	50 (125)	12 (287)
Previous WR Ad. Female	33 (88)	3 (218)	38 (226)	12 (885)
	*	**	***	n.s.
Unringed Ad. Male	90 (91)	39 (297)	91 (193)	65 (961)
Present WR Ad. Male	85 (85)	30 (353)	90 (203)	52 (693)
Previous WR Ad. Male	71 (389)	30 (1513)	85 (1395)	48 (7174)
	***	**	*	***

*** P<0.001, ** P<0.01, * P<0.05

7.3.3b Consistency of individual dominance measures

Dyadic encounters can be combined further to calculate the proportion of dyads that were won by an individual. I refer to this proportion henceforth as the 'win proportion', although several varieties of win proportion are used. For example, win proportions could be measured against any of the four age/sex categories or subsets of these (e.g. versus females), or could be measured on an annual or a lifetime basis. The win proportion (WP) of an individual bird was defined as:

$$WP = \frac{\text{no. of dyads won} + (0.5 \times \text{no. of dyads drawn})}{\text{no. of dyadic encounters}}$$

for any subset of opponents (e.g. juvenile males in 1990/91, all females, etc.). The win proportion therefore varied between 0 and 1, with low WPs indicating that few dyadic encounters were won, and high WPs indicating that most dyadic encounters were won. Wherever appropriate, WPs were arcsine transformed in order to normalise the data. Furthermore, an individual's win proportion was only used in an analysis if it was based on a minimum of five dyadic encounters.

It is important to establish whether win proportions measure some aspect of aggression or dominance of an individual accurately and consistently. I approached this firstly by examining whether or not variation in win proportions was caused by chance, and secondly by testing whether birds that had high WPs against one age/sex category also had high WPs against other age/sex categories.

Appleby (1983) demonstrates that a linear or near-linear ordering of individuals in a dominance hierarchy can be obtained relatively easily by chance alone, even though the direction of relationships between individuals is random. He also, however, provides details of a procedure for calculating the probability that the rank ordering of a set of individuals in a dominance hierarchy is due to chance. If an observed rank ordering of individuals is unlikely to have occurred by chance, we can be confident that a high-ranking individual is more likely to be successful against a low-ranking individual than expected by chance, even though the two individuals may never have interacted. In other words, relationships between individuals are not random, but can be predicted by the outcome of their relationships with other individuals.

To test whether or not the relationships between Snow Buntings were random, I selected those adult males which were observed interacting with other adult males on at least 50 occasions, and in at least three of the five winters in which aggression was recorded. These criteria removed age and sex effects and ensured that all birds had a chance of interacting with each other. In total, 19 adult males satisfied these criteria and were arranged according to the percentage of the selected birds they dominated in dyadic encounters (**Table 7.8**).

Table 7.8. Dominance hierarchy among nineteen frequently recorded adult male Snow Buntings. *Individuals ('GNRM', 'NOMR', etc.) become more dominant from top to bottom and from left to right of the table. Right of the diagonal, 'O' represents dyadic encounters which were successfully predicted by the listed hierarchy, 'X' represents dyads whose outcome was opposite to that predicted, '+' represents dyads that were drawn, and blanks represents pairs of birds which never interacted.*

	G N B M G Y R O R O G M N R Y G O N R		
	N O Y B T S Y N O B N B Y S O N R Y G	% of dyads won:	
	R M B N G R M M G L M B G R O M M B O	within this	with all
	M R M Y M M Y B M M Y N M M M S G M M	group	adult males *
GNRM	- O O O O O O O O O O O O O	0	8
NOMR	- + O O + O X O O O O O O O	21	28
BYBM	- + + O X O O + O O O O O O O O	22	21
MBNY	- O + + O + + O X O O O O O	25	40
GTGM	- O X O + O + X O O O O	35	49
YSRM	- X + O O X O O O O O +	40	36
RYMY	- X X + O X O O O O O O	41	36
ONMB	- X X X O O O O O	43	42
ROGM	- X X X O O O O O O O	44	51
OBLM	- X O X O O X O O	46	44
GNMY	- O X X O O X + O	50	46
MBBN	- X X O O	50	46
NYGM	- + X O O O O	59	52
RSRM	- O X X X	62	64
YOOM	- O O O O	72	57
GNMS	- O O O	76	61
ORMG	- X	77	66
NYBM	- O	78	69
RGOM	-	96	88

* Win Proportion when Adult against all adult males (see 7.3.3d)

Amongst these 19 males, only 28 (16%) of the possible 171 combinations of birds failed to interact. Such incomplete information reduces the probability that the linearity of the hierarchy will be significant (Appleby 1983). Nevertheless, Appleby's General Test for linearity in the hierarchy was highly significant ($X^2_{26}=56.8$, $P<0.001$; see Appleby 1983 for test procedure). Therefore the outcome of contests between given pairs of individuals is predictable from the outcomes of their contests with other birds: some birds are relatively dominant whereas others are typically subordinate. Furthermore, the rank order established amongst these 19 birds was strongly correlated to their win proportion against all adult males (and hence their estimated competitive ability - see **7.3.3d** for more details; $r_s=0.93$, $n=19$, $P<0.001$).

The degree of linearity of this hierarchy, indicated by the coefficient K (Appleby 1983), was 0.35. K varies between 0, when all relationships are random, and 1, when the hierarchy is completely linear (i.e. no dominance reversals occur). In total, the direction of 23% of the 127 dyads with definite outcomes was opposite to that expected, indicating that subordinates defeated more dominant birds relatively frequently. Not unexpectedly, most of these reversals occurred between birds which were relatively similar in status, as indicated by the relative abundance of dominance reversals close to the diagonal in **Table 7.8**. Altogether, 34% of the 803 separate interactions between these 19 birds resulted in a win for the bird of *lower* dominance rank.

As it was also possible that birds varied their agonistic effort depending on the relative rank of their opponents (see Slotow *et al.* 1993 for discussion of like-versus-like fighting; also **7.3.4** and **7.4.2**), I also calculated the correlations between individuals' WPs against one age/sex category and their WPs against other age/sex categories. **Table 7.9** lists the annual number of birds of a given age/sex category for which a win proportion could be calculated (i.e. they were involved in at least five dyadic encounters) against the same or another age/sex category. The bias of birds present (see **Chapters 4 & 5**), and the high percentage of contests involving adult males (**Table 7.1**), inevitably led to a greater number of win proportions being calculated for adult males or against adult males. Conversely relatively few data were available for juvenile females. For any winter where, for a given age/sex category, there was at least five individuals with calculated WPs against two or more categories of opponent, I plotted the WP of each individual against one category of opponent versus its WP against the other age/sex categories. **Fig.7.10** shows the comparison with most data: juvenile males in winter 1988/89 with high WPs against fellow juvenile males were also likely to have high WPs against adult males. **Table 7.10** gives the regression statistics for all 15 such comparisons with sufficient data.

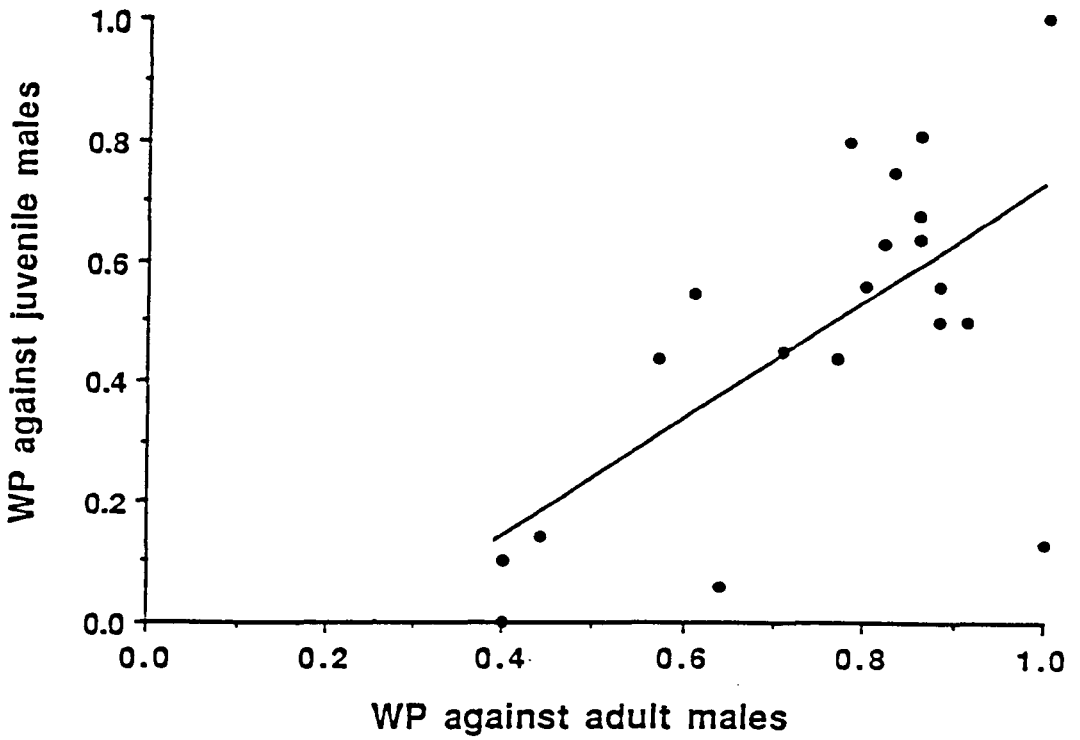


Fig.7.10. The proportion of dyadic encounters won by focal juvenile male Snow Buntings in 1988/89 against their fellow juvenile males plotted against the proportion they won against adult males. *Focal birds which had higher win proportions against juvenile males also had greater success against adult males (for arcsine transformed data, r=0.61, P=0.004; the fitted regression line is also significant but was calculated from the untransformed proportions).*

Table 7.9. The number of Snow Buntings in each age/sex category per annum which had five or more dyadic encounters against an age/sex category of opponent.

		Age/sex category of opponent:				
Year	Age/sex of individual	Juvenile Female	Juvenile Male	Adult Female	Adult Male	Σ
1988/89	Juvenile female		1		1	2
	Juvenile male	1	24	7	20	52
	Adult female		7	1	7	15
	Adult male		18	4	16	38
1989/90	Juvenile female		1		2	3
	Juvenile male		8	1	12	21
	Adult female		1	2	10	13
	Adult male		13	10	27	50
1990/91	Juvenile male				8	8
	Adult female				11	11
	Adult male		5	10	44	59
1991/92	Juvenile female		3	2	7	12
	Juvenile male	2	1	2	8	13
	Adult female				9	9
	Adult male	4	6	5	35	50
1992/93	Juvenile male			1	6	7
	Adult female			2	7	9
	Adult male		5	12	28	45
Σ	Juvenile female		5	2	10	17
	Juvenile male	3	33	11	54	101
	Adult female		8	5	44	57
	Adult male	4	47	41	150	242
	Σ	7	93	59	258	417

Table 7.10. The correlations between an individual Snow Bunting's win proportion against two different categories of age/sex of opponent. *n is the number of focal individuals that interacted with five or more individuals from the two opponent age/sex categories. All proportions were arcsine transformed prior to the correlation analysis.*

Age/sex of focal individuals	Age/sex of opponent categories:		Year	n	r	P
Ad.female	Juv.male	Ad.male	1988/89	5	-	- *
Juv. male	Juv.male	Ad.female	1988/89	7	-0.35	0.44
Juv. male	Ad.female	Ad.male	1988/89	7	-0.41	0.36
Juv. male	Juv.male	Ad.male	1988/89	20	0.61	0.004
Juv. male	Juv.male	Ad.male	1989/90	8	0.66	0.07
Ad.male	Juv.male	Ad.female	1989/90	6	0.97	0.002
Ad.male	Ad.female	Ad.male	1989/90	9	0.30	0.44
Ad.male	Ad.female	Ad.male	1990/91	10	0.55	0.10
Ad.male	Ad.female	Ad.male	1991/92	5	0.28	0.65
Ad.male	Ad.female	Ad.male	1992/93	12	0.66	0.02
Ad.male	Juv.male	Ad.male	1988/89	13	0.31	0.31
Ad.male	Juv.male	Ad.male	1989/90	12	0.76	0.004
Ad.male	Juv.male	Ad.male	1990/91	5	0.84	0.08
Ad.male	Juv.male	Ad.male	1991/92	6	0.60	0.21
Ad.male	Juv.male	Ad.male	1992/93	5	0.60	0.28

*** not calculated - all WPs versus juvenile males were zero.**

As expected if individual dominance is positively associated across age/sex categories of opponents, more of the correlations in **Table 7.10** are positive than expected by chance (Binomial test, P=0.012). Moreover, four of the correlations were significant in their own right (two more with P<0.1). Therefore, despite the small samples in most cases, there is good evidence that, amongst males at least, the proportion of encounters an individual won against one age/sex category was positively related to the proportion it won against another age/sex category. This indicates that an individual's relative WP against one age/sex category should consistently indicate its relative dominance against all other birds.

7.3.3c Individual changes in win proportion between years

Given the large number of adult males which were involved in aggression in relation to the other age/sex categories (**Tables 7.1 & 7.9**), and the finding that win proportions of individuals were positively related across age/sex categories (**7.3.3b**), I simplified many of the remaining analyses by just using the (transformed) win proportion of individuals against adult males as an index of their dominance status.

Table 7.11 shows the average win proportion against adult males of each of the age/sex categories per annum. Within sexes, win proportions were similar between years, but even when the data were aggregated to this degree, the average win proportion of a juvenile bird was higher than the average for a same-sex adult bird (ANOVA, including year as a factor: effect of age in females, $F_{1,46}=16.1$, $P<0.001$; in males, $F_{1,194}=26.0$, $P<0.001$). The win proportion of juvenile females against adult males was 0.26 higher than that of adult females. Because adult females had a win proportion of only 0.07, juvenile females were almost five times more likely than adult females to win a dyadic encounter against an adult male. Similarly the WP of juvenile males was 0.27 higher than that of adult males, and they were 60% more likely to win a dyadic encounter against an adult male. Clearly juvenile individuals were, on average, dominant to adults of the same sex.

There are three possible reasons for this result. Firstly, only dominant juveniles may have been able to become established on Cairn Gorm in their first winter (but see **7.4.4**). Secondly, dominant juveniles may have been less likely to return to Cairn Gorm in subsequent winters (see **9.3.4 & 7.4.4**). Thirdly, the win proportion of juveniles may be lower when they return in subsequent winters. I will next address this third possibility.

The win proportion against adult males of 28 Snow Buntings (25 males, 3 females) was known in both their first and a subsequent winter. An individual's win proportion as a juvenile was positively related to its win proportion as an adult (**Fig.7.11**; $r_{26}=0.45$, $P=0.016$), indicating that birds which won more encounters in their first winter were also more likely to win encounters when older. However, a pairwise t-test indicated that on average the win proportion of an individual as an adult was also *lower* than its WP as a juvenile ($t_{27}=2.27$, $P=0.03$). The mean difference between the WP of an individual as a juvenile and its WP as an adult was 0.11, but this varied according to the actual value of the WP (due to the arcsine transformation): birds with WPs near 0.5 as juveniles would have WPs about 0.16 lower as adults, but birds nearer the ends of the dominance scale would show smaller changes. This is sufficient to explain about half of the observed difference between the win proportions of juveniles and adults (see **Table 7.11**).

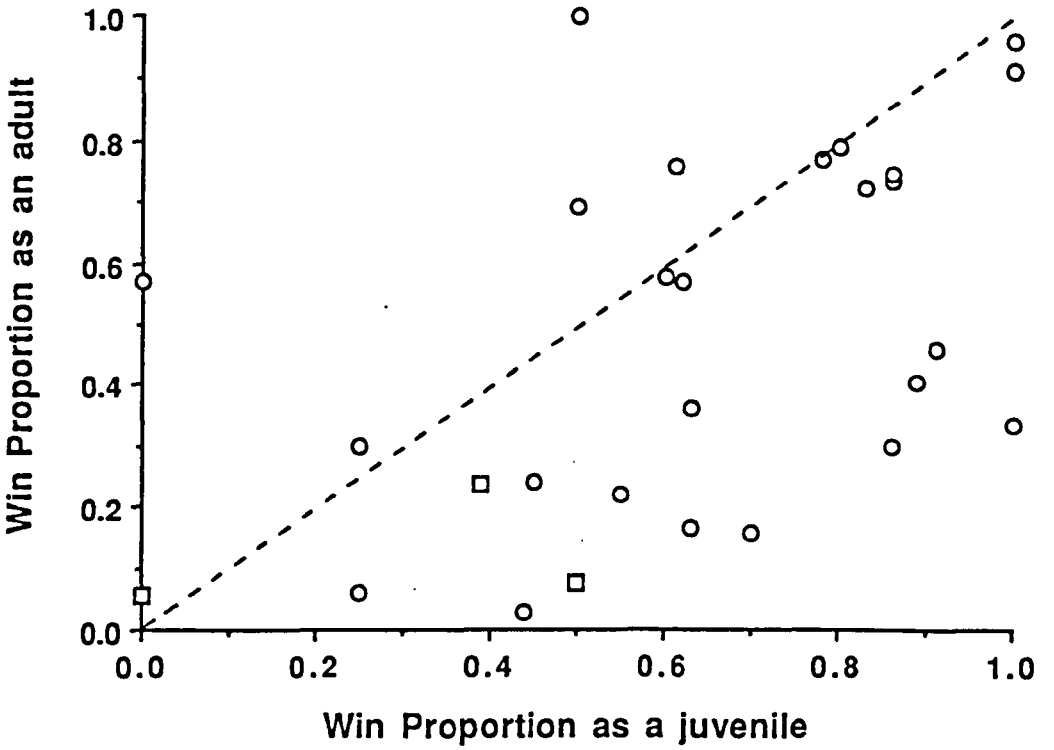


Fig.7.11. The win proportion against adult males of Snow Buntings when adult against the win proportion of the same birds when they were juveniles. *Females are indicated by squares, males by circles. Although the correlation is significant (see text) the more important item to note is that the points are significantly below the line of equality (t_{27}=2.27, P=0.03). An individual's win proportion was therefore on average* lower *when it returned as an adult.*

Table 7.11. The mean annual win proportion of each of the four age/sex categories of Snow Buntings against adult males. *The averages given here are back-transformed actual proportions, after taking averages from the arcsine transformed proportions of each contributing individual. The win proportion of adult males are slightly lower than the expected 50% because experienced adult males won less contests than inexperienced ringed birds (see **2.3.3a**), and experienced adults were more sedentary (see **9.3.1** & **9.3.2**) and hence more likely to interact with at least five other adult males. Sample size in brackets is the number of individuals.*

Age/sex category	1988/89	1989/90	1990/91	1991/92	1992/93	Σ
Juvenile female	.64	.39		.27		.33
	(1)	(2)	(0)	(7)	(0)	(10)
Adult female	.04	.03	.16	.04	.08	.07
	(7)	(10)	(11)	(9)	(7)	(44)
Juvenile male	.78	.58	.79	.66	.75	.72
	(20)	(12)	(8)	(8)	(6)	(54)
Adult male	.46	.43	.44	.47	.48	.45
	(16)	(27)	(44)	(35)	(28)	(150)

The win proportion against adult males was also known in two or more winters for 37 adult birds (32 males, 5 females) with previous site experience in both winters, and 6 birds (4 males, 2 females) which were inexperienced adults in the first winter present (**Fig.7.12**). For both groups the correlation between an individual's WP in the winter when it was first measured and the winter when it was next measured was positive, again indicating some consistency in individual dominance between years (for experienced adults in first year: $r_{35}=0.63$, $P<0.001$; for inexperienced adults in first year: $r_4=0.72$, $P=0.11$). There was no tendency for either experienced or inexperienced adults to show reduced dominance when returning in subsequent winters (**Fig.7.12**; paired t-tests for experienced adults, $t_{36}=0.25$, $P=0.80$; for inexperienced adults, $t_5=0.05$, $P=0.96$).

Was there any evidence of consistent changes in win proportion with age *per se*, apart from between juvenile and adulthood, perhaps indicative of senescence? I measured the win proportion of 23 birds of

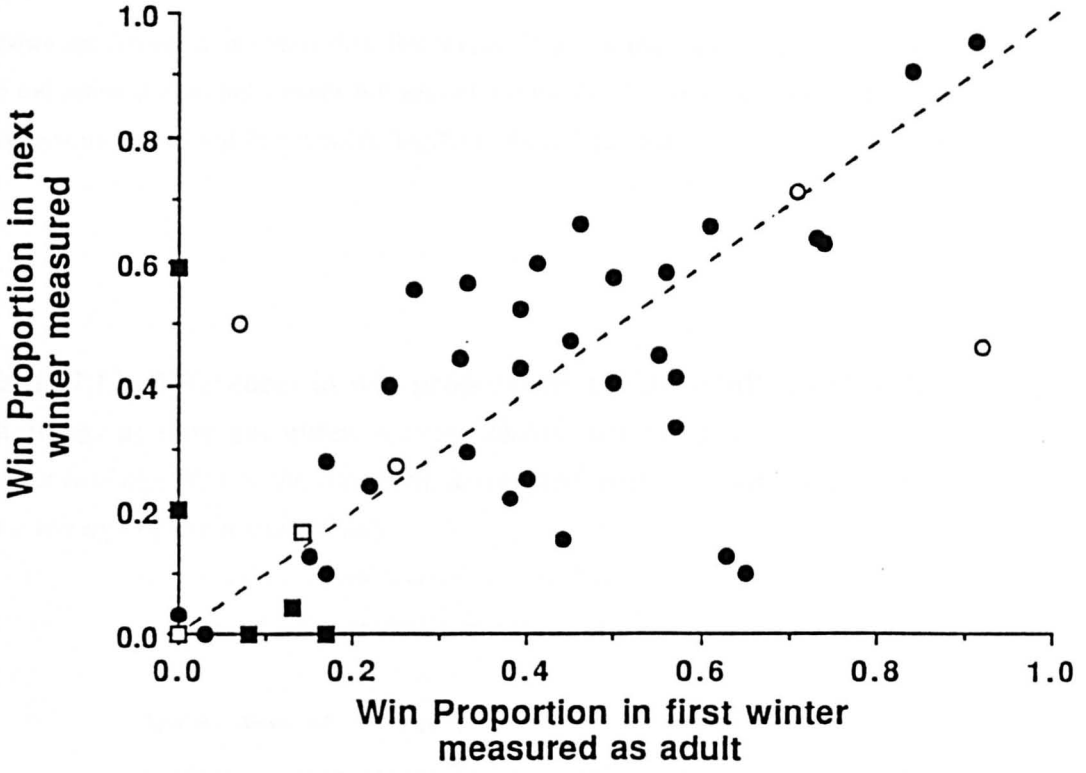
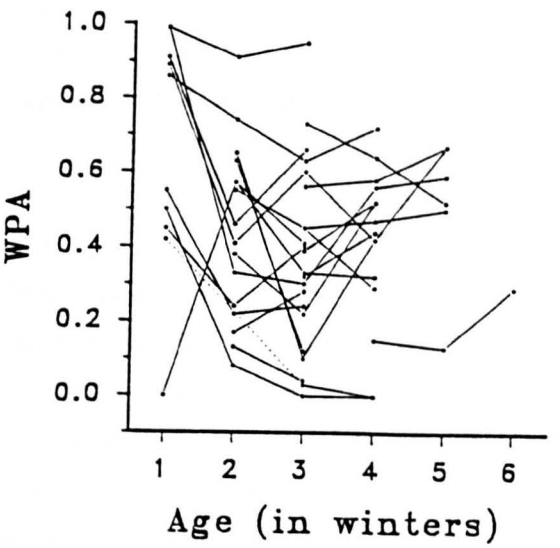


Fig.7.12. The win proportion against adult males of individual adult Snow Buntings in the first winter it was measured against that in the following or subsequent winters. *Filled symbols represent birds which had previous site experience in both winters, while open symbols indicate those with no previous site experience in the first winter. Squares represent females, circles males. Note that, unlike* ***Fig.7.11****, points are distributed evenly about the line of equality, indicating that an individual's win proportion was similar in both winters.*

Fig.7.13. Change in win proportion against adult males of known age Snow Buntings as they got older. *Solid lines indicate changes from one winter to the next, the dashed line shows a change over two winters. Changes from the first to the second winter are only shown if data was also available from the third winter - see* ***Fig.7.11*** *for further changes between individuals' first and second winters. There is a significant decrease between the first and second winters (see* ***Fig.7.11****) but no significant change thereafter (see* ***Table 7.12****).*



known age (ringed in or before their first winter) in two or more winters after their first winter. There was no indication that an individual's WP against adult males showed a consistent upward or downward trend between its second and fifth winters (**Fig.7.13, Table 7.12**), although sample sizes were small.

Table 7.12. Differences in win proportions against adult males of known-age Snow Buntings as they got older. *n is the sample size of birds with win proportions at both age A and age B; t is the t-statistic associated with a paired t-test of the win proportions at each age of the n individuals.*

Pair of ages being compared:

Age A,	Mean WP	Age B,	Mean WP	n	t	p
2	0.43	3	0.33	16	1.69	0.11
2	0.45	4	0.38	8	1.18	0.28
3	0.33	4	0.39	14	1.08	0.30
3	0.52	5	0.59	5	0.76	0.49
4	0.46	5	0.50	6	0.83	0.44

7.3.3d Defining WPA, the proportion of dyadic encounters won as adults.

As there was no evidence of further changes in win proportion with age after the first year (**7.3.3c**), I defined a special category of win proportion which will be used extensively throughout the remainder of this thesis to compare birds of different competitive ability. Dyadic encounters against adult males were summed each winter for all birds. If an individual's dyadic encounters were always recorded when the individual was itself an adult, these dyads were summed and an overall win proportion calculated. If some or all dyadic encounters were recorded when the individual was a juvenile, I calculated its WP as a juvenile and its WP as an adult, corrected its WP as a juvenile to that expected when it became adult (using the

average decrease in win proportion of 28 individuals outlined in **7.3.3c**, using transformed data thereby reducing the differences in win proportion of birds near the end of the spectrum by less than those in the middle), and then took an average value, weighted by the sample size of dyadic encounters at each age. I refer to this win proportion henceforth as the win proportion when adult or WPA, and used its arcsine transformed derivative whenever parametric tests were needed.

7.3.3e Does dominance depend on the location of the encounter?

To examine this possibility, I selected all adult males that had participated in at least 10 encounters with other adult males at each of at least two bait locations. All four sites with relevant data were between 630 and 2660m apart in horizontal distance and between 65 and 530m apart in altitude (see **Fig.2.1**). The percentage of encounters that a male won was positively correlated between each pair of sites and four of the six comparisons were significant (**Table 7.13**; Combined Probabilty Test, $X^2_{12}=47.4$, $P<0.001$). Therefore, because individuals did not appear to be dominant at one site yet subordinate at others, there was no evidence that dominance was site-related in Cairn Gorm-wintering Snow Buntings.

Table 7.13. The correlation between an individual adult male Snow Bunting's percentage of encounters won against adult males at one Cairn Gorm baiting site, and its percentage of encounters won at a different site. *n is the sample size of males with 10+ interactions against other adult males at each pair of sites.*

	% won at PTB			% won at CCPB			% won at CCTB		
	r	n	P	r	n	P	r	n	P
% won at CIFS	0.47	11	0.14	0.83	34	<0.001	0.72	9	0.029
% won at PTB				0.63	8	0.09	0.88	5	0.046
% won at CCPB							0.79	7	0.030

7.3.3f Is dominance related to body-size?

I have already established that most males are dominant to most females (**7.3.3a**). This may, however, have been a result of their larger body size rather than gender. I therefore investigated the possibility that dominance was related to body-size *per se*, by looking for a relationship between win proportion when adult (WPA) and wing-length *within* sexes.

On average the longest-winged birds (corrected for age - see **3.3.3** & **8.2.1**) of either sex had wings 15% longer than the shortest-winged birds of the same sex, while the difference between the 25th and 75th percentiles in a given gender was 2.9% (n=1612 females, 777 males). This latter value is approximately half of the 5.5% difference in wing-length *between* the sexes found by Banks *et al.* (1989), or the 6.3% difference found in the present study (using data derived from **Table 3.3**). Because the difference in dominance between the sexes was substantial (**7.3.3a**), I would therefore still expect to find some indication of size-related dominance within the sexes if dominance was largely based on size rather than gender. However, regressions of wing-length on WPA were insignificant in both sexes (females: r_{35}=-0.11, P=0.53; males: r_{94}=0.004, P=0.97). There was therefore no evidence within gender for size-related differences in dominance.

7.3.3g Are local breeders dominant over immigrants?

Altogether, 18 of the 130 males of known win proportion when adult (WPA) were local breeders (in the Cairngorms - see **2.6**). These might have had an aggressive advantage over winter immigrants because of prior residency. Alternatively, they might have been more aggressive because higher dominance status may have helped attract potential mates. However, the mean WPAs of local breeders and winter immigrants were similar (0.51; using transformed data, $F_{1,128}$=0.002, P=0.96), suggesting that local breeders are not dominant over immigrants in winter. Only one local breeder persistently chased off other males from a baited site. This was a male in its first breeding season which held the nearest breeding territory to the bait site, approximately 2km away. It chased away other males (but not two females) from CCPB during a late snowfall on 13th-15th May 1993. All of its victims, and both females, were also local breeders. No such behaviour had been noted from the same individual during numerous sightings in March and early April 1993.

7.3.3h Do dominance relationships change in bad weather?

Several studies have observed changes in the outcome or characteristics of contests following manipulation of the value of a resource. If the value of a resource is increased for some individuals, these may become more likely to win contests against unmanipulated individuals (e.g. Popp 1987a, Andersson & Ahlund 1991). At Cairn Gorm, bad weather may have increased the value of resources to all birds present because

it resulted in increased energy demands or made food less accessible. The outcome of contests might therefore change if birds only show their true agonistic potential when resource values are higher, i.e. in severe weather. In particular, given their greater feeding efficiency (**6.3**), adults may gain less than juveniles from contests in mild weather, and hence show a tendency to defer to juveniles. But in severe weather we might see an increase in the proportion of contests won by adults because access to food may become more important to them.

I assumed that lower temperatures, higher winds, deeper snow and greater amounts of snow cover were worse foraging conditions for Snow Buntings. I therefore looked for an association between worsening weather and changes in the proportions of contests won by each of the age/sex categories, changes in the direction of individual dyads between juvenile and adult males, and changes in win proportion amongst adult males. **Table 7.14** indicates how the weather variables were categorised for these analyses. Although for some variables the majority of aggressive interactions were recorded in 'severe' weather, I would still expect to see an increase in the proportion of contests won by adults or males in severe weather, even if they only realised their full agonistic potential in a fraction of the worst conditions. Note anyway that most observations were made in weather which was worse than average (**Table 7.14**).

There was little consistent difference in the proportion of contests won between the age/sex categories in relation to weather conditions (**Fig.7.14**). No weather variable was consistently associated with a greater likelihood of victory under harsh conditions for adults or males. Furthermore, where the age/sex categories differed in the proportion of encounters won under different conditions of a given weather variable (7 of the 36 comparisons were significant), in only one case was an increase in the proportion of encounters won by an adult or a male associated with the most severe weather conditions (**Fig.7.14**). The outcome of contests between adult males and adult females did appear to be associated with weather to some extent, but, contrary to the prediction that the 'best' birds sometimes deferred to weaker birds in mild conditions, adult males were *less* likely to win contests with adult females during partial or complete snow cover (**Fig.7.14**).

I also examined my data for evidence that the dominance of *individual birds* changed in harsh weather conditions. I chose to restrict this analysis to adult males to avoid any complications between age and sex categories. I used the win proportion when adult of these birds to define overall dominant, intermediate and subordinate adult males (WPAs of >0.6, 0.4-0.6 and ≤ 0.4 respectively). For males with five or more dyadic encounters in both 'good' and 'bad' weather conditions, I compared the number of birds which in bad conditions showed increases in win proportion with the number of birds which showed decreases, using Wilcoxon matched pairs tests (**Table 7.15**). There was no indication that intermediate or dominant birds showed changes in win proportion in worse weather, although subordinate adult males showed slight (but insignificant) increases in win proportion in snowier conditions.

Table 7.14. Categorisation of weather variables for aggression analyses. *Increasing 'severity' indicates that I would expect foraging conditions to become more difficult for foraging Snow Buntings. In certain analyses the conditions were redefined simply as good (G) or bad (B). The percentage of days with a given weather condition was calculated from weather conditions during October to April each year. Details of how weather conditions were measured are given in 2.3. The date of interactions was only recorded in winters 1989/90-1992/93; sample sizes for each weather variable (final two columns respectively) are therefore 10726 interactions and 850 days.*

Weather variable	Severity		Description:	% of observed contests in given conditions:	% of days with given conditions:
SNOW DEPTH	0	G	No lying snow	19	64
	1	G	1-9cm of snow	24	18
	2	B	10-20cm of snow	37	13
	3	B	> 20cm of snow	19	5
WIND SPEED	0	G	< 25mph	44	51
	1	B	≥ 25mph	56	49
SNOW COVER	0	G	Ground snow/ice free	10	42
	1	G	Partial snow/ice cover	18	34
	2	B	100% snow cover	72	24
SNOW COVER PREV.DAY	0	G)	as previous variable	20	42
	1	G)	but using value from	22	34
	2	B)	the previous day	58	24
9AM TEMPERATURE	0	G	9 a.m. temp. ≥ 0°C	42	79
	1	B	9 a.m. temp. < 0°C	58	21
MEAN TEMPERATURE	0	G	Mean temp > 1.5°C	25	63
	1	G	Mean temp -1.5 to 1.5°C	41	28
	2	B	Mean temp < -1.5°C	34	9

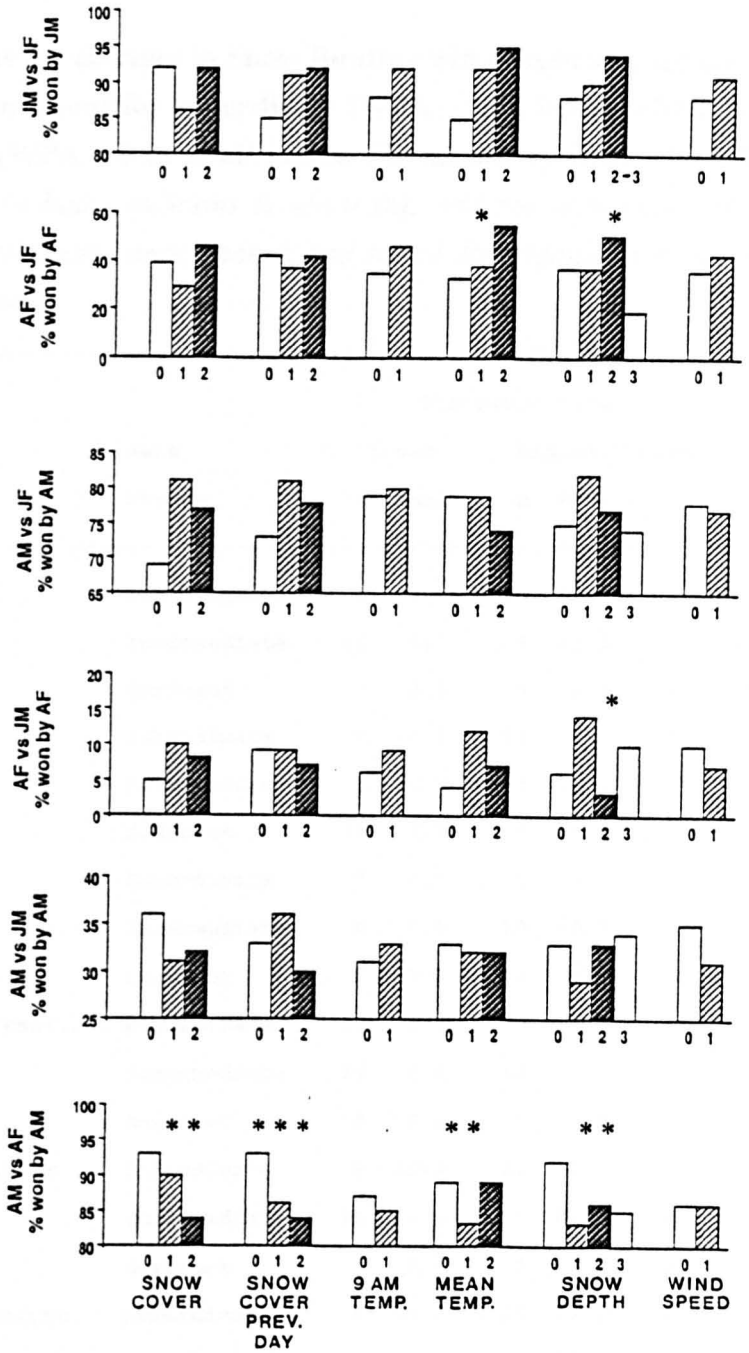


Fig.7.14. The percentage of contests won by older Snow Buntings (or males if similar in age) in relation to weather conditions. *Adult male is abbreviated to AM, juvenile female to JF, etc. Sample sizes for each of the six age/sex category comparisons are (from top to bottom) 230, 209, 536, 421, 1817 & 1668 contests. Significance levels are those associated with chi-square tests under the null hypothesis that the number of contests won by the focal age/sex category is similar in all categories of the given weather variable (***=P<0.001, **=P<0.01, *=P<0.05, otherwise n.s.). The categories of each of the six weather variables are plotted from left to right in order of increasing weather severity (see* ***Table 7.14****). Therefore if older (or male) Snow Buntings won more interactions in harsh conditions, the bars would tend to slope up to the right in each weather variable. No such consistent effect is discernible along weather variables or across age/sex categories.*

Table 7.15. Tests for changes in Snow Bunting win proportion against adult males in bad weather conditions for subordinate (WPA ≤ 0.4), intermediate (WPA = 0.4-0.6) and dominant (WPA > 0.6) adult males. *The number of birds with a higher or lower win proportion in bad conditions is given (n), and the differences in win proportion according to conditions were ranked and tested for significance using the Wilcoxon matched pairs test.*

		Win proportion:					Wilcoxon	
Weather	Male	lower		higher		tied	test:	
Variable:	Status	n	Rank	n	Rank		z	P
SNOW DEPTH	Subordinate	8	8.8	14	13.1	1	1.83	0.07
	Intermediate	10	9.7	9	10.3	1	0.08	0.94
	Dominant	9	8.6	8	9.5	0	0.02	0.98
WIND SPEED	Subordinate	7	10.1	10	8.2	0	0.26	0.79
	Intermediate	9	8.5	8	9.6	2	0.00	1.00
	Dominant	10	9.3	8	9.8	0	0.33	0.74
SNOW COVER	Subordinate	7	6.1	8	9.6	0	0.97	0.33
	Intermediate	8	8.9	10	10.0	1	0.63	0.53
	Dominant	6	7.5	8	7.5	0	0.47	0.64
SNOW COVER PREV.DAY	Subordinate	10	9.4	7	8.5	1	0.80	0.42
	Intermediate	10	8.4	10	12.6	0	0.78	0.43
	Dominant	8	8.2	8	8.8	0	0.10	0.92
9AM TEMPERATURE	Subordinate	8	13.2	12	8.7	1	0.04	0.97
	Intermediate	11	10.1	9	11.0	0	0.22	0.82
	Dominant	8	6.6	7	9.6	1	0.40	0.69
MEAN TEMPERATURE	Subordinate	6	13.0	16	10.9	0	1.57	0.12
	Intermediate	8	10.1	11	10.0	2	0.58	0.56
	Dominant	8	11.8	11	8.7	0	0.02	0.98

Finally it is possible that although the relative proportions of victories remained consistent within age/sex categories, this was achieved because different birds were present in good and bad conditions. I therefore examined the outcome of dyads between juvenile males and adult males which interacted in both good and bad conditions. I predicted a *reduction* in the proportion of dyads won by juvenile males in bad conditions, under the hypothesis that adults only showed their true potential in severe weather. However, the data did not support this possibility: for five of the six weather variables considered, juveniles won slightly *more* dyadic encounters in bad conditions compared to good conditions (**Table 7.16**).

In summary, there was little evidence that adults or males 'hold back' in aggressive encounters with juveniles or females in milder spells of weather. The tendency for juveniles to dominate adults therefore appears stable and unrelated to weather conditions. Although it is still conceivable that the direction of dominance could change in exceptionally severe conditions, the hierarchical order of dominance observed is unlikely to have changed much over the vast majority of conditions experienced during the study winters.

Table 7.16. The percentage of dyadic encounters won by juvenile male Snow Buntings against the same adult males in good versus bad conditions. *n is the sample size of dyads. None of the differences approach significance (all P>0.1).*

Weather variable:	n	% dyads won in: Good conditions	Bad conditions	X^2_1
SNOW DEPTH	59	68	65	0.01
WIND SPEED	55	65	69	0.16
SNOW COVER	60	66	74	0.63
SNOW COVER PREV.DAY	68	65	76	2.27
9AM TEMPERATURE	60	68	72	0.09
MEAN TEMPERATURE	65	63	69	0.55

7.3.4 Do interactions occur randomly?

Although **7.3.1b** suggests that in a given time period juvenile males were most likely to initiate aggressive interactions, and adult females were most likely to be targeted, this does not necessarily tell us that high status birds tended to target low status birds. To investigate whether the frequency of contests between birds of different dominance status deviated from a random expectation, I examined firstly whether or not high ranking birds of a given age/sex category were more likely than low ranking birds to interact with adult males of a particular status (as measured by win proportion when adult, WPA), and secondly whether adult males of a particular status were more likely to interact with females or juvenile males than other adult males.

To perform the first of these analyses, I selected those individuals which interacted with ten or more adult males of known WPA. I then worked out for each individual the mean WPA of its opponents in these contests (weighting the WPA of each opponent by the number of contests between them), and plotted this against the individual's own WPA.

Amongst adult males, a negative correlation was expected even if birds interacted at random (because the number of adult male competitors is limited, and birds cannot interact with themselves, therefore the WPA of opponents of subordinates would be slightly greater than the mean WPA, and vice versa for dominants). To control for this I assumed that the dominance hierarchy was linear with birds interacting at random. Then, an individual's expected mean opponent WPA is calculated as:

$$\frac{\text{sum of all n individuals' WPAs minus the focal bird's WPA}}{n-1}$$

The mean number of ranked opponents that each eligible bird encountered was 25. This is, of course, a conservative measure of the number of *potential* opponents it could face. Therefore, using the above equation, I would expect that if 26 birds interacted at random in a linear hierarchy, the mean WPA of the opponents of the most subordinate (WPA=0) and most dominant individual (WPA=1) would be 0.52 and 0.48 respectively. I then calculated a residual score for dominance class of opponents (WPA of opponents minus expected WPA of opponents). There was a significant negative relationship between an individual's WPA and the residual WPA of its opponents, i.e. dominant adult males interacted with subordinate adult males more often than expected (**Fig.7.15**; r_{66}=-0.25, P=0.048).

I used a similar analysis to investigate whether or not there was comparable variation in the dominance status of adult male opponents of adult females or juvenile males. I could find no evidence, however, that dominant individuals amongst these two other age/sex categories interacted more frequently than expected with relatively subordinate adult males, or vice versa (adult females: r_s=0.02, P=0.95; juvenile males: r_{17}=-0.19, P=0.44).

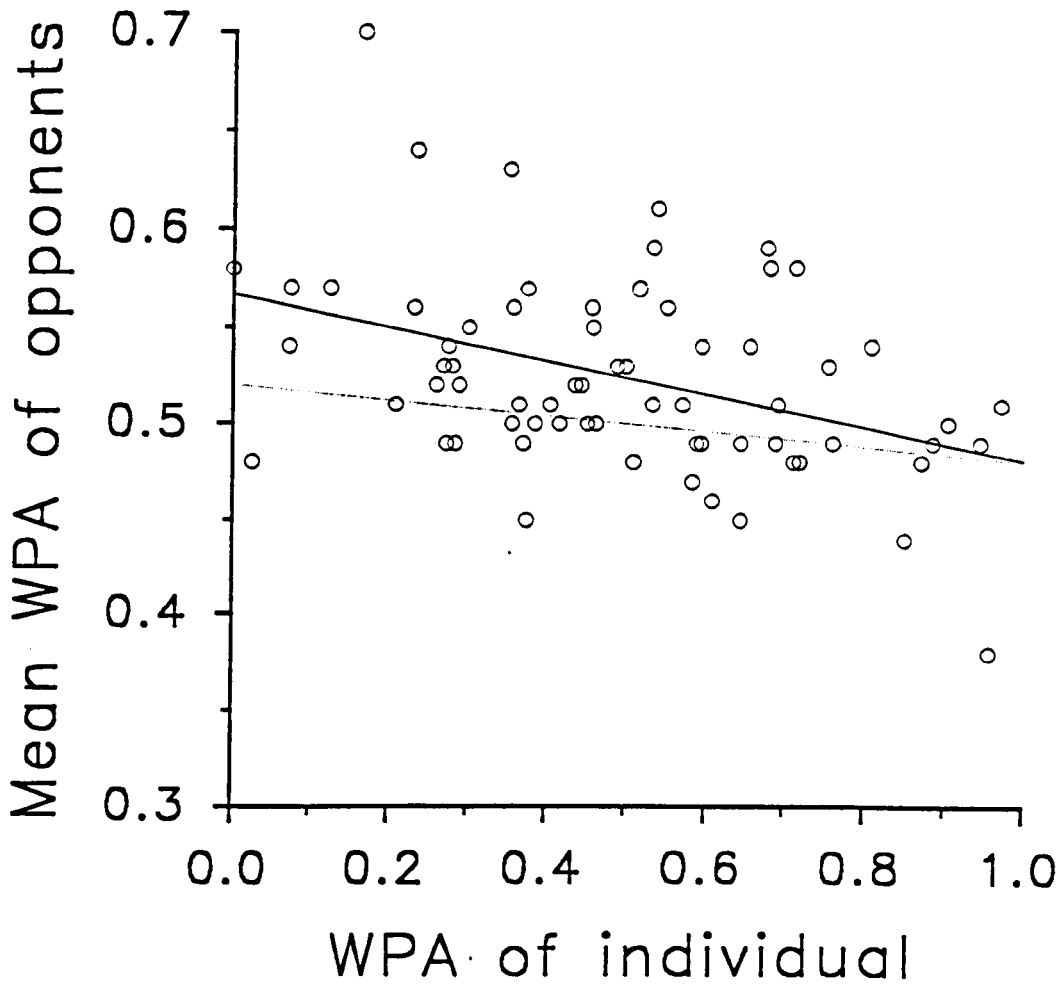


Fig.7.15. The average WPA of an adult male Snow Buntings's adult male opponents (weighted by the number of contests) in relation to the adult male's own WPA (solid regression line). *Only males which interacted with at least ten other adult males of known WPA were included (n=68). The dashed line represents the expected WPA of adult male opponents if birds chose opponents at random (see text). The residual differences between the regression line and the dashed line are significant (following arcsine transformation), indicating that adult males interacted with other adult males of similar status less often than expected (see text for details).*

The proportion of interactions against other age/sex categories would be expected to vary with the proportion of the other age/sex categories present in the population. I therefore worked out the frequency with which each adult male interacted with females and juvenile males, as a proportion (arcsine transformed) of all the encounters in which it participated each winter. I then selected adult males for which more than ten interactions were noted during a winter, and grouped them by WPA (grouped as in **7.3.3h**: dominant, intermediate and subordinate adult males with WPAs of >0.6, 0.4-0.6 and ≤0.4 respectively). YEAR (i.e. winter 1988/89, 1989/90, etc.) was also included as a control variable because small annual differences in population composition were recorded (**5.3.1**). I then tested for differences between adult male dominance categories in the proportion of their interactions which involved females or juvenile males. There was no indication that the adult male dominance categories differed in their likelihoods of facing females (mean=18% of contests, n=160 male-winters; ANOVA, effect of year, $F_{4,145}=10.3$, $P<0.001$; effect of WPA, $F_{2,145}=0.11$, $P=0.9$, interaction term n.s.). The same test, performed on the number of contests against juvenile males, gave a significant result for the interaction of YEAR and WPA (i.e. there was significant annual variation in the degree to which adult male dominance was associated with variation in the proportion of opponents that were juvenile males). However, within years, the only significant result was that in 1991/92 subordinate adult males tended to interact more often against juvenile males than intermediate or dominant adult males (25% versus 12% of contests; oneway ANOVA, $F_{2,32}=4.60$, $P=0.02$). In none of the other four winters in which aggression was recorded, did subordinate adult males interact more frequently than dominant adult males against juvenile males. Therefore the evidence that dominance rank affects the frequency with which adult males interact with the other age/sex categories is, at best, weak.

7.3.5 Contest characteristics - initiation, possession and intensity

7.3.5a Contests between Dominants and Subordinates

The win proportion when adult (WPA) was known for both contestants in 3252 (49%) of the 6637 contests in which full characteristics (Attacker, Possessor and type) of the interaction were recorded. In the present section, Dominants were defined simply as birds having greater WPAs than their opponents (who were thus defined as Subordinates).

Interactions could be divided into two categories according to the 'possession status' of the initiator, i.e. whether or not it already had access to the resource contested (Possessor or Intruder respectively, following the terminology of Senar *et al.* 1989). Consequently a bird engaging in a contest had one of four possible roles to play. It could initiate the contest when already in possession of a resource (ATTACKER-POSSESSOR), it could initiate when not holding the resource (ATTACKER-INTRUDER), it could be attacked whilst possessing the resource (TARGET-POSSESSOR), or it could be attacked when not possessing a resource (TARGET-INTRUDER).

The majority (84%) of the 3252 contests were initiated by birds not holding the contested resource. A contestant was much more likely to win the contest if it was the Attacker and less likely to win it if it was the Possessor (success rate of Attacker=85%, test of difference from random: $X^2_1=1602.7$, $P<0.001$; success rate of Possessor=30%, $X^2_1=493.6$, $P<0.001$). However, if a bird was the Attacker it was *more* likely to win the contest as an ATTACKER-POSSESSOR (99% won, n=514) than as an ATTACKER-INTRUDER (82% won, n=2738; $X^2_1=97.2$, $P<0.001$). Restating this result in a different manner, TARGET-POSSESSORs were more likely to win contests than TARGET-INTRUDERs, so after controlling for who started the interaction, the Possessor of the resource was more likely to win than the Intruder.

Dominant individuals won 77% of all interactions. Given that most encounters were won by initiators (above), it was perhaps not surprising that Dominants initiated a much larger proportion of contests than Subordinates (74% versus 26%, $X^2_1=957.9$, $P<0.001$). Nevertheless, the results given in the previous paragraph largely held for both Dominants and Subordinates (**Table 7.17**), indicating that initiation of an encounter was more important to its outcome than the perceived dominance status of the contestants. The only differences were that Dominants still won the majority of their contests when they were Possessors (although they won a lower proportion of contests than if they had been Intruders; $X^2_1=275.0$, $P<0.001$). Consequently Subordinates won a minority of encounters when Intruders (although winning a greater proportion than if they had been Possessors). Also, the importance of possession status varied with dominance status: although both Dominants and Subordinates won significantly less of the contests that they initiated when they were Intruders, reduced success was particularly noticeable in Subordinates (**Fig.7.16**). Despite this, in contests where Subordinates were Possessors (n=2091), they were initiated by the Subordinate on only 5% of occasions; in contrast, when Dominant Possessors interacted, 35% (n=1161) were self-initiated ($X^2_1=514.1$, $P<0.001$). However, this may have been because Subordinate Possessors suffered a greater rate of being supplanted. Nevertheless, there was also evidence that for focal Attackers, Subordinates were less likely to initiate contests as Possessors (as a percentage of all contests initiated) than Dominants: Subordinates were the Possessors in only 12% (n=855) of the contests which they initiated, whereas Dominants were the Possessors in 17% (n=2397; $X^2_1=11.2$, $P<0.001$).

Table 7.17. Percentage of encounters won by Dominant or Subordinate Snow Buntings in relation to whether they Attacked or were Targets, and whether they Possessed a resource or Intruded on it. *The sample size of contests is given in brackets. Significance is calculated from the null hypothesis that initiation or possession did not affect the outcome of the contest (chi-square test). Note that for Attacker/Target and Possessor/Intruder comparisons the significance tests of diagonally opposite values are the same (and hence redundant), but the values are included for clarity.*

	Percentage won if:			
Status	Attacker	Target	Possessor	Intruder
Dominant	92 ***	35 ***	61 ***	86 ***
	(2397)	(855)	(1161)	(2091)
Subordinate	65 ***	8 ***	14 ***	39 ***
	(855)	(2397)	(2091)	(1161)

*** P<0.001

7.3.5b Age/sex differences in contest characteristics

In this section I consider the 1107 contests between juvenile and adult male Snow Buntings, and the 2213 contests between males and females, in which full characteristics of the encounter were recorded. These contests were chosen because they offered a comparison between interactions contested by more and less evenly-matched contestants respectively (as judged by the percentage of encounters won by the dominant age or sex category, see **Tables 7.6 & 7.18**) than those in the previous analysis. Because many of these contests involved unringed birds or birds whose colour-rings were not fully identifed, or birds which did not interact with a sufficient number of adult males for their WPA to be calculated, only 52% of the 1107 interactions between males and 32% of the 2213 interactions between the sexes were included in the previous section (forming only 39% of the previous sample). Therefore there was considerable scope for variation from the previous results.

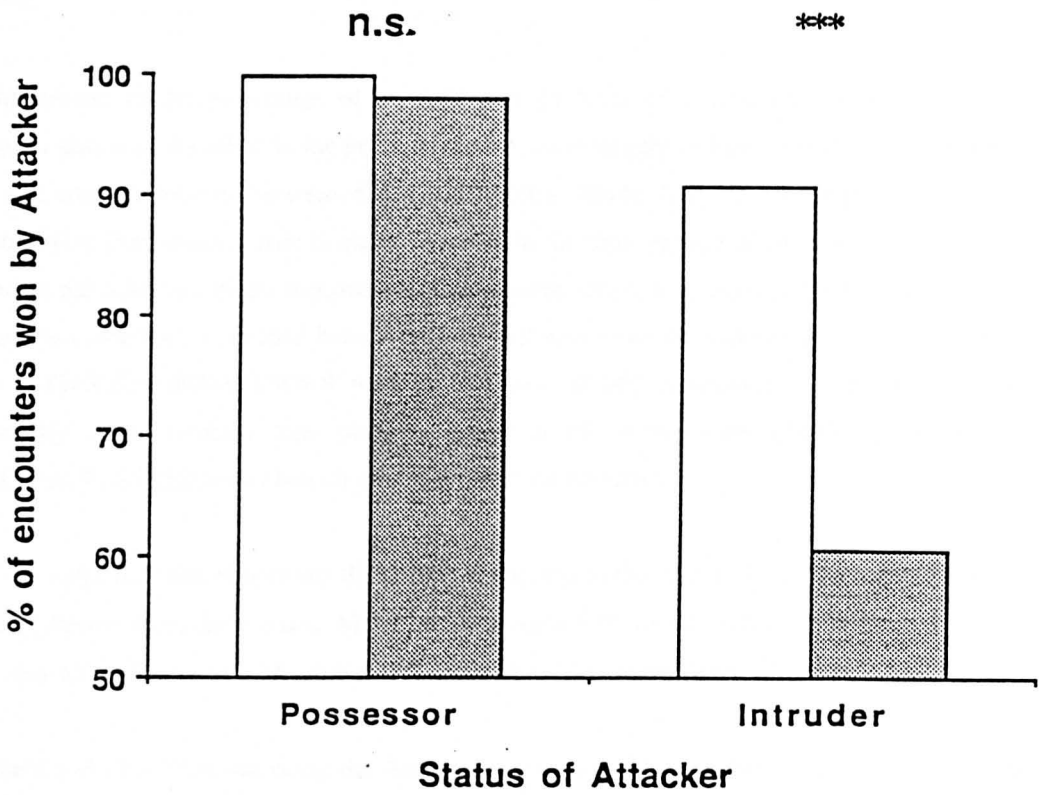


Fig.7.16. The percentage of Snow Bunting contests won by Attackers in relation to their possession status and dominance status. *Blank bars show the percentage of encounters won by initiating Dominants, stippled bars those won by initiating Subordinates. Significance levels are those associated with a chi-square test for a difference in the proportion of contests won by Dominants or Subordinates of a given role. Sample sizes (left to right) are 410, 104, 1987 & 751 contests.*

The competitors were ranked in order of increasing likelihood of winning a contest against their designated opponents (females versus males and vice versa; juvenile males vs adult males and vice versa). Females were thus the lowest ranked of the four categories, then adult males. Juvenile males were higher and males (versus females) highest. Relative Status, defined as the rank of the Winner minus the rank of the Loser, would on average be most negative in contests won by females and greatest in contests won by males. The value would be intermediate in contests won by adult males and juvenile males, although slightly higher in the latter.

The differences in the percentage of contests won by birds of contrasting dominance, initiation or possession status, as described in the previous section, were largely reflected in contests between juvenile males and adult males, and between males and females (**Table 7.18**). In all comparisons the dominant contestant (i.e. Dominants, juvenile males or males in the three groups of contests) won the majority of encounters but Attacking birds, irrespective of dominance status, won more. In females, the lowest ranked birds of the contestants examined here, Attackers still won some 66% of encounters with males; indeed female ATTACKER-POSSESSORS won all but two of 265 encounters. As expected, males won significantly more contests than juvenile males in all comparisons (**Table 7.18**) except when ATTACKER-POSSESSORs (when all dominants won all contests).

There were also differences between the groups of contests in the relative frequency of initiation between birds of different dominance status. Males initiated some 87% of all contests with females, but juvenile males only 65% of contests with adult males (n=2213 & 1107 respectively, $X^2_1=219.7$, $P<0.001$).

The likelihood of a Possessor being the Attacker in a contest increased with Relative Status (**Fig.7.17**), indicating either that birds with the lowest relative rank were least likely to start a contest when holding a resource, or were most likely to be challenged in this situation. Although there was a significant difference between contestants in the relative frequency with which they initiated contests as ATTACKER-POSSESSORs (as opposed to ATTACKER-INTRUDERs) this was not associated linearly with Relative Status (**Fig.7.18**; $X^2_3=13.6$, $P<0.01$). Instead, initiation from a resource-holding position was associated more often than expected with juvenile males.

Table 7.18. Comparison of percentages of contests won in relation to a Snow Bunting's dominance, initiation, possession and role within a contest for groups of interactions with different categories of actors. *Dominants were birds of higher WPA than their opponents (Subordinates), and a full description of characteristics of contests between these birds is given in* ***7.3.5a****. The percentage of contests won by Dominant and Subordinate actors is merely repeated here for illustrative purposes. In contests between juvenile and adult males, and between males and females, juvenile males and males respectively were considered to be dominant (see text). The chi-square statistic is based on the null hypothesis that there was no difference between these latter two groups of interactions in the percentage of contests won by the category of bird given in the first column. All percentages of contests won by a category of bird in any column differ significantly from 50% at P<0.001, i.e. there was a directional bias in success for all categories of birds given in column 1. Sample size of contests in brackets.*

	Contests between:				
% of contests won by:	Dominants & Subordinates	Juv. & adult males	Males & females	X^2_1	P a
Dominants	77 (3252)	73 (1107)	88 (2213)	116.15	***
All Attackers	85 (3252)	82 (1107)	92 (2213)	64.18	***
Dominant Attackers	92 (2397)	93 (716)	96 (1921)	10.77	**
Subordinate Attackers	65 (855)	64 (391)	66 (292)	0.24	n.s.
All Possessors	30 (3252)	32 (1107)	20 (2213)	59.84	***
Dominant Possessors	61 (1161)	56 (469)	67 (491)	13.06	***
Subordinate Possessors	14 (2091)	15 (638)	6 (1722)	40.61	***
All ATTACKER-POSSESSORs	99 (514)	99 (166)	99 (265)	0.22	n.s.
Dominant A-Ps	100 (410)	100 (122)	100 (232)	0.00	n.s.
Subordinate A-Ps	98 (104)	96 (44)	94 (33)	0.09	n.s.
All ATTACKER-INTRUDERs	82 (2738)	80 (941)	91 (1948)	71.09	***
Dominant A-Is	91 (1987)	91 (594)	95 (1689)	13.29	***
Subordinate A-Is	61 (751)	60 (347)	62 (259)	0.31	n.s.

*** P<0.001; ** P<0.01; * P<0.05; n.s. not significant

a Probability that the % of encounters won by the given actor (column 1) is the same for juvenile/adult male actors and male/female actors.

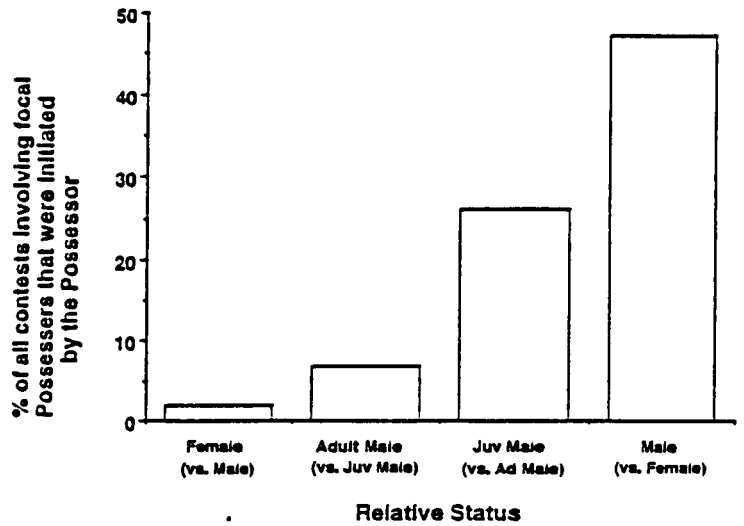


Fig.7.17. The frequency of contests which focal Possessor Snow Buntings initiated (as a percentage of all contests in which they became involved) in relation to the focal bird's Relative Status (see text). *The percentage of contests initiated by focal Possessors increased with Relative Status (chi-square test: $X^2_3=788.5$, $P<0.001$). Sample sizes (left to right) are 1722, 638, 469 & 491 contests.*

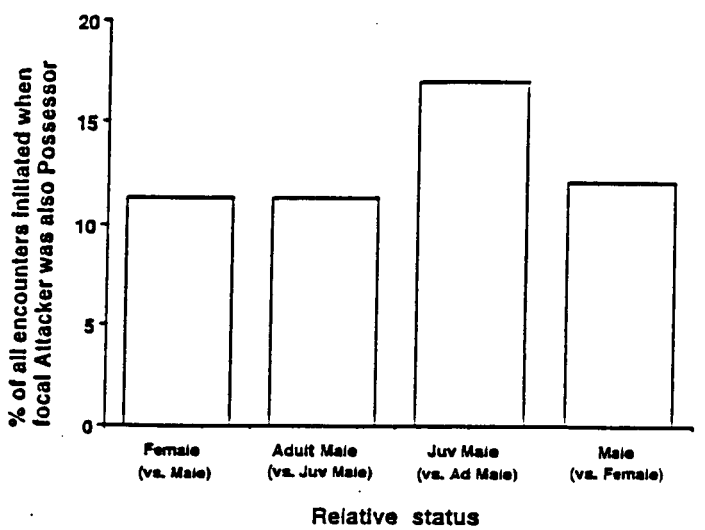


Fig.7.18. The frequency of contests initiated by focal ATTACKER-POSSESSOR Snow Buntings (as a percentage of all contests initiated by focal Attackers) in relation to the focal bird's Relative Status. Juvenile males initiated a significantly greater percentage of contests when in possession than other focal Attackers (chi-square test: $X^2_3=13.6$, $P<0.01$). Sample sizes (left to right) are 292, 391, 716 & 1921 contests.

7.3.5c Characteristics of escalation

A total of 287 interactions recorded on video-film were studied in greater depth. The majority (89%) were initiated by a 'lunge' from the Attacker into the area (within a body-length) of the Target. The other 11% involved 'intimidation', when the Attacker approached the Target but stopped short of a body-length, or faced the Target with partly-open mandibles. Apart from this latter behaviour, the Attacker did not appear to display in any conspicuous way which forewarned the Target of its impending approach.

Nevertheless, physical contact with Targets on the first approach was rare, occurring in 34% of Fights and only 6% of all 287 contests. Only two of the 17 contacts on first approach did not appear to be anticipated - in the other 15 the Target was able to meet its Attacker with its own bill. This suggests that the type of contest (whether or not it was escalated) was mainly determined by the Target: whether it chose to avoid the Attacker's advance immediately (as happened in 72% of the 287 contests), or stand its ground and/or retaliate (causing a physical contact Fight in 62% of the remaining 80 contests). Avoiding the Target's counter-lunge may have been less easy because, by this stage, the contestants were usually within one body-length of each other: 67% of the 33 Fights which did not involve contact on the first approach *did* involve contact as a result of the first counter-lunge from the Target. Only four of the 50 Fights had not involved contact after three behavioural elements (i.e. Attacker's approach, Target's response, Attacker's counter-response), and all Fights had involved contact by the fifth behavioural element.

Returning to the sample of fully described interactions between Dominants and Subordinates (as described in **7.3.5a**), 26% (out of 3252) were Fights. In these, I would expect to see an increase in the percentage of contests won by Targets on occasions when they chose not to avoid the Attacker immediately. Because the number of behavioural elements was not routinely recorded (elements were difficult to separate even on slow-motion video-film), I predicted that Targets would win Fights (always more than one behavioural element) more often than Threats (often only one behavioural element). Perhaps inevitably, this was true (37% vs 7%, n=845 & 2407; $X^2_1=430.8$, $P<0.001$). As a consequence of this, a contest developed into a Fight on only 19% of occasions when the Attacker won, but on 64% of occasions when the Target was the victor.

The contest was no more likely to have been a Fight if won by an ATTACKER-INTRUDER than an ATTACKER-POSSESSOR (20% versus 17% of 2257 & 511 contests respectively, $X^2_1=1.57$, n.s.). Despite this, only ATTACKER-INTRUDERs showed a significant decrease in the percentage of contests won if these became Fights (**Fig.7.19**). In other words, ATTACKER-POSSESSORs still almost invariably won even if fights became escalated, whereas ATTACKER-INTRUDERs only had a high success rate if the interaction did not escalate.

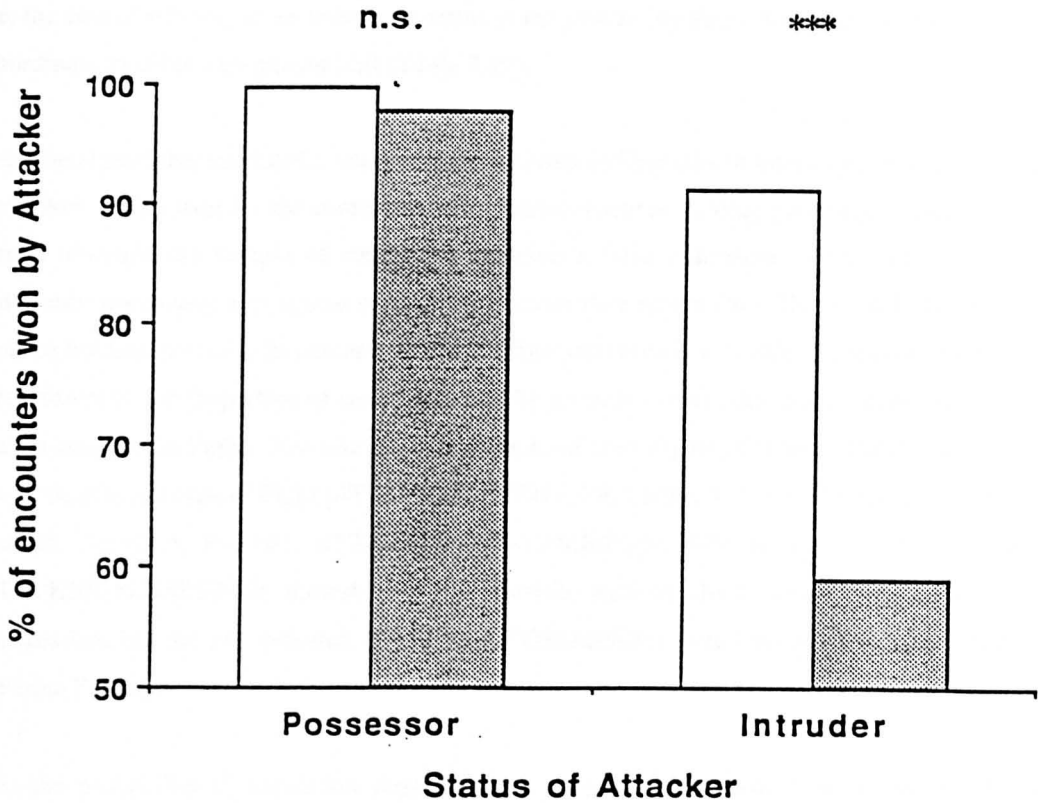


Fig.7.19. The percentage of contests won by Snow Buntings which initiated contests in relation to their possession status and whether or not the contest became escalated (i.e. involved physical contact). *Blank bars show the percentage of encounters which were Threats, stippled bars those which were Fights. Significance levels are those associated with chi-square tests for a difference in success rate with degree of escalation. Sample sizes (left to right) are 424, 90, 1983 & 755 contests.*

7.3.5d Escalation in relation to dominance status

As in the previous section, escalation reduced the probability that ATTACKER-INTRUDER Snow Buntings (but not ATTACKER-POSSESSORs) would win encounters, irrespective of dominance status (**Table 7.19**). However, contests which became Fights were not always won by the Dominant bird. Indeed, Subordinate ATTACKER-INTRUDERs and ATTACKER-POSSESSORs still won 40% & 97% of Fights respectively (n=299 & 29). However, after controlling for possession status, contests with Subordinate Attackers were more likely to escalate than those with Dominant Attackers (**Table 7.19**), i.e. Dominant Targets were less likely than Subordinate Targets to give way immediately. This meant that, for a given role, the cost of winning an encounter (in terms of the probability that it would escalate) was greater for a Subordinate than for a Dominant bird (**Table 7.19**).

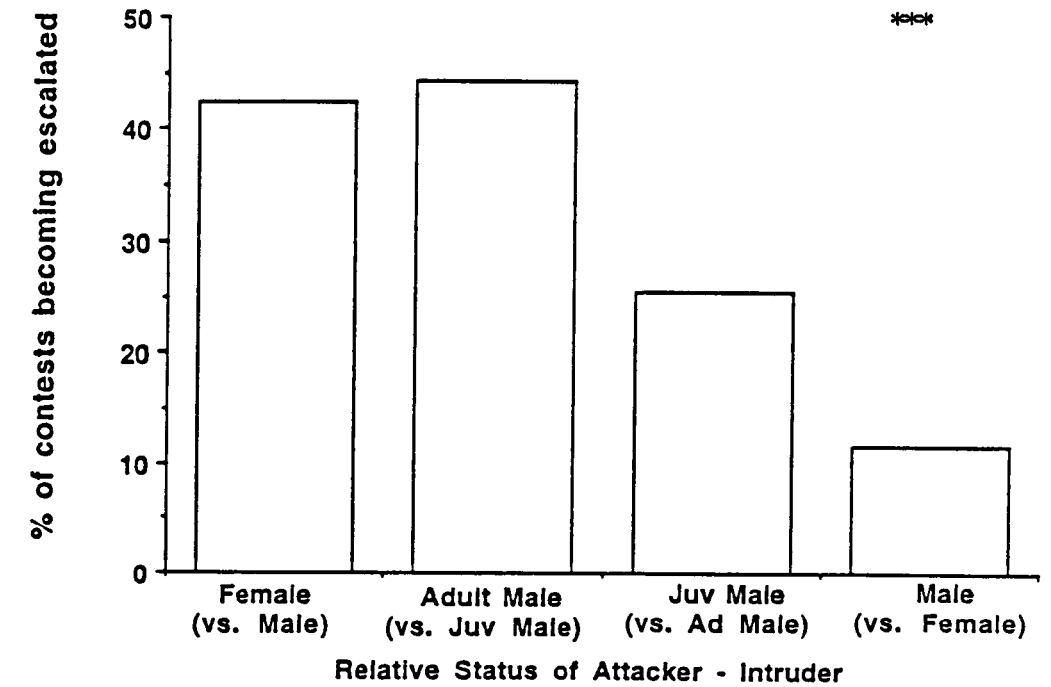
It may be argued that escalated contests, where the costs and benefits of interacting may be higher, may be more likely to be won by the contestant with greater resource holding potential. Perhaps by including Threats amongst my sample of contests, I obtained a false indication of the relative dominance of contestants: dominants may appear subordinate because they retreat from Threats and only show their true resource holding potential in contests where the contested resource is valuable enough to cause them to fight. However, the proportion of encounters won by juvenile versus adult males, compared to vice versa, was not reversed in Fights. Juvenile males won more of their Fights with adult males than vice versa for any given role and type of Fight (ATTACKER-INTRUDER/Threat, 97% won by juvenile versus 75% won by adult, $X^2_1=74.5$, $P<0.001$; ATTACKER-INTRUDER/Fight, 74% vs 42%, $X^2_1=30.5$, $P<0.001$; for ATTACKER-POSSESSORs, almost all contests (n=166) were won by initiators irrespective of dominance or escalation, but the two defeated ATTACKER-POSSESSORs were both adult males, including one of only nine Fights).

Does the probability of escalation depend on the size of the difference in dominance between the competitors? I again selected only contests between the sexes (ignoring age) and contests between the ages in males (as in **7.3.5b**) as a largely independent sample of contests from that used in **Table 7.19** (see caveats in **7.3.5b**). In these contests, increasing Relative Status of an age/sex category which Attacked was associated with a reduced probability that contests would become escalated (**Fig.7.20**). Because Attackers still won a large number of escalated contests, this reduced frequency of escalation gradually decreased the likelihood that a contestant would have to Fight in order to win a contest as Relative Status increased (**Fig.7.21**). Hence, for a given role, the relatively most subordinate birds appeared to have the highest (and dominants the lowest) costs of winning.

Table 7.19. The success rate of Dominant or Subordinate Snow Buntings when initiating encounters, and the percentage of contests won by Attackers, according to their possession status and the degree of escalation of the contest. *Fights, unlike Threats, involved physical contact. The number of contests is given in brackets. Significance levels are those associated with chi-square tests between the two separated percentages.*

Attacker:	% of contests escalated	% contests won by Attacker if Threat		Fight	% of contests which were Fights if won by Attacker	Target
Subordinate	40	74	***	40	26	60
ATTACKER-INTRUDER	(751)	(452)		(299)	(455)	(296)
	***				***	*
Dominant	23	96	***	72	18	70
ATTACKER-INTRUDER	(1987)	(1531)		(456)	(1802)	(185)
Subordinate	28	99	n.s.	97	27	-
ATTACKER-POSSESSOR	(104)	(75)		(29)	(102)	(2)
	**				**	
Dominant	15	100	n.s.	98	15	-
ATTACKER-POSSESSOR	(410)	(349)		(61)	(409)	(1)

*** P<0.001, n.s. P>0.1



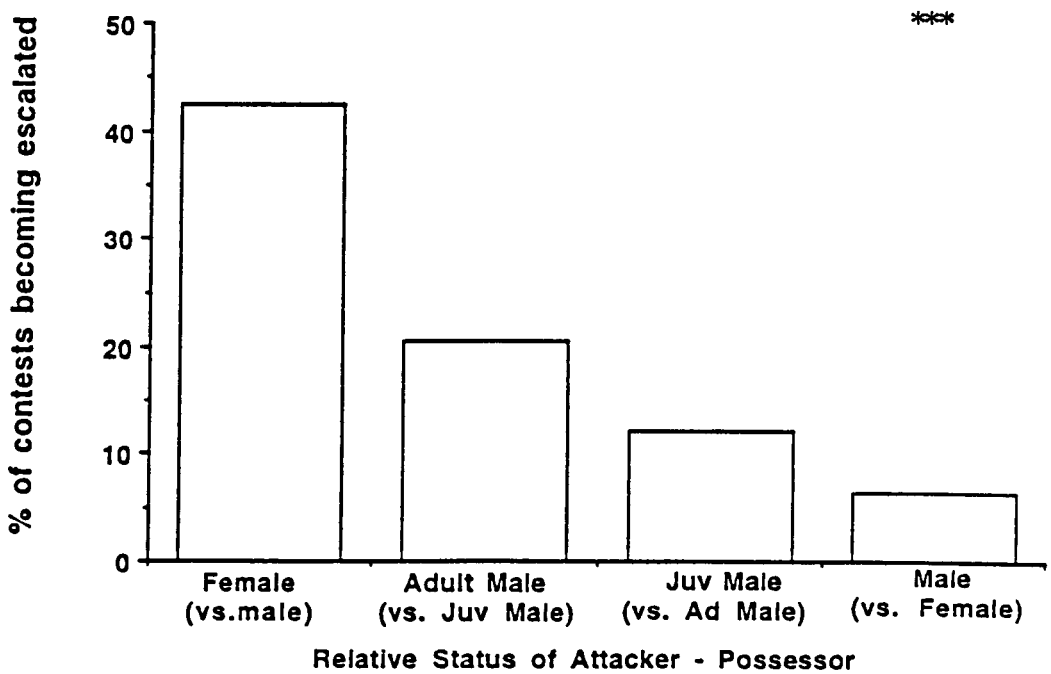


Fig.7.20. The percentage of contests that became escalated in relation to the Attacker Snow Bunting's Relative Status. *The significance levels are those associated with chi-square tests for differences in the height of the bars (3 d.f., *** = P<0.001). Sample sizes (left to right, top to bottom) are 259, 347, 594, 1689, 33, 44, 122 & 232 contests. The general decrease in escalation from left to right (within possession classes) shows that dominant Attackers were less likely to face retaliation than subordinate Attackers.*

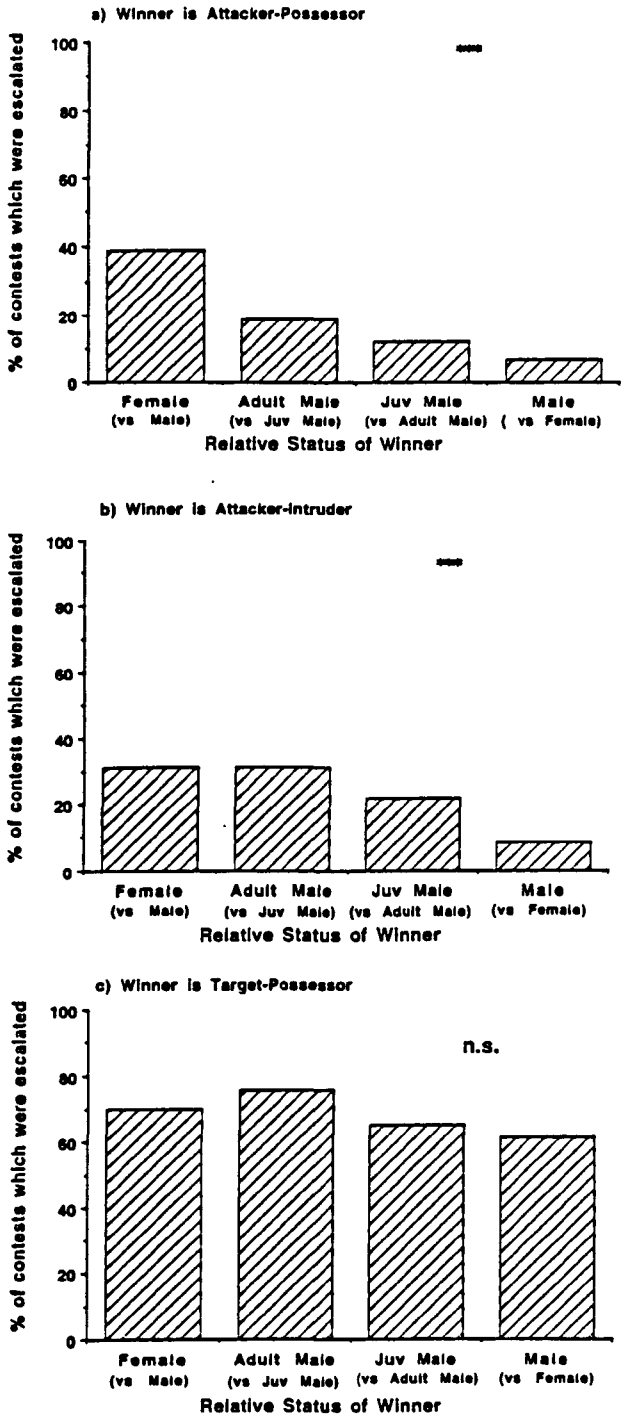


Fig.7.21. The percentage of contests that became escalated in relation to the winning Snow Bunting's Relative Status and role. *The significance levels are those associated with chi-square tests comparing the frequency of escalation between Relative Status categories (3 d.f., *** = P<0.001). Sample sizes (left to right, top to bottom) are 31, 42, 122, 232, 161, 208, 541, 1609, 80, 53, 139 & 98 contests. The general decrease in escalation from left to right (within roles) shows that dominants require less effort to win contests than subordinates.*

Because, for a given role, the costs of winning contests (in terms of escalation) were least for birds which had the greatest advantage in dominance status over their opponents (**Fig.7.21**), and the most dominant birds were most likely to play the least costly Attacking roles (**7.3.5b**), I expected that the costs of winning any contest would be least for birds with the greatest dominance advantages over opponents. Returning therefore to the larger sample of contests, which included those where the roles of the contestants were not always noted, I found support for this. Contests were most likely to be Threats if the Winner was of a considerably higher dominance status than the Loser. Moreover, Long Fights, involving 3+ seconds of physical contact, were usually between evenly matched birds (**Fig.7.22**; $F_{2,5345}=79.7$, $P<0.001$). The likelihood of escalation decreased steadily as the winner's dominance status (as measured by WPA) increased above that of the loser (**Fig.7.23**). This also held for contests between the age/sex categories (**Fig.7.24**). The frequency of escalation was negatively correlated to the dominance advantage that the winning age/sex category held over its opponent ($r_{14}=-0.93$, $P<0.001$).

In contests between two birds of the same age/sex category, age did not influence contest intensity but males were more likely to become involved in escalated encounters than females (**Fig.7.25**; loglinear test: significance of interaction between contest type and sex, $X^2_1=16.8$, $P<0.001$; contest type x age, $X^2_1=0.18$, $P=0.67$; 3-way interaction term, $X^2_1=0.87$, $P=0.35$).

7.3.5e Escalation in relation to weather and patch size

Did more contests escalate as resource value increased in bad weather? Perhaps energy conservation at such times would reduce the likelihood of escalation? Weather conditions were categorised as Good or Bad for six variables as indicated in **Table 7.14**. Because of the effect of dominance on the likelihood of escalation (**7.3.5d**), I controlled for differences between contestants by looking for a consistent pattern of change in escalation across the 16 pairs of winning/losing age/sex categories.

Contests were significantly more likely to be Fights on days with mean wind speeds of 25mph or more (Wilcoxon matched pairs test: $z=2.16$, $P=0.03$). However, there was no difference in the percentage of contests escalated in Good versus Bad conditions for any of the other five weather variables (all $P>0.2$).

Finally, since patch-size and flock-size were known to affect the likelihood of aggression occurring (see **7.3.1**), I examined the influence of these variables on contest escalation using the same data set as in **7.3.1b**. I could find no evidence, however, that patch-size or flock-size affected the degree of escalation of contests although sample sizes were small (**Table 7.20**; loglinear chi-squares associated with removing the given interaction terms from the model describing my data: Patch-size*Flock-size*Escalation, $X^2_2=3.49$, $P=0.18$; Patch-Size*Escalation, $X^2_1=0.17$, $P=0.68$; Flock-size*Escalation, $X^2_2=0.47$, $P=0.79$).

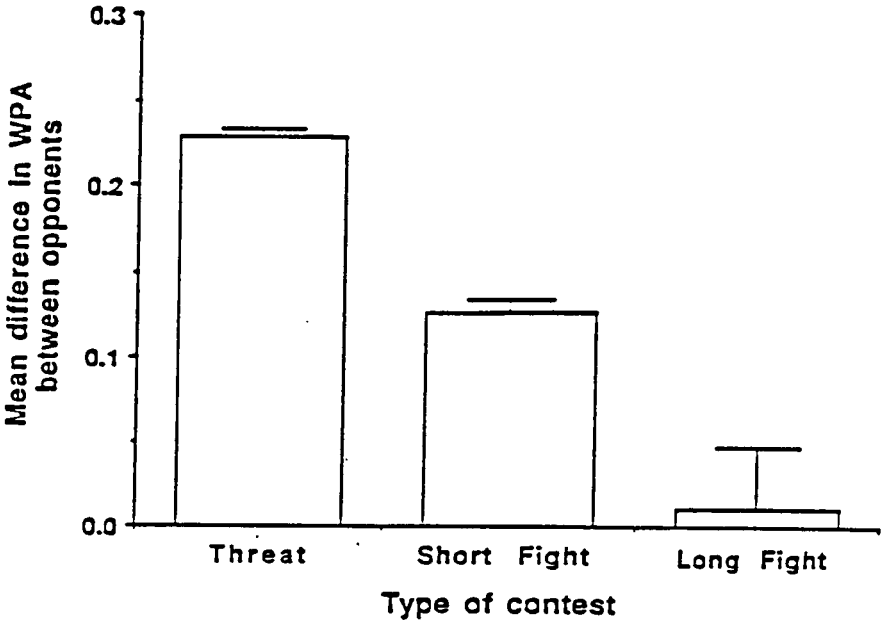


Fig.7.22. The degree of escalation of Snow Bunting contests in relation to the difference in WPA between the Winner and Loser (WPA of Winner minus WPA Loser). *Threats involved no physical contact, Short Fights had some physical contact and Long Fights involved 3+ seconds of physical contact. Standard error bars are given. Sample sizes (left to right) are 3656, 1621 & 71 contests.*

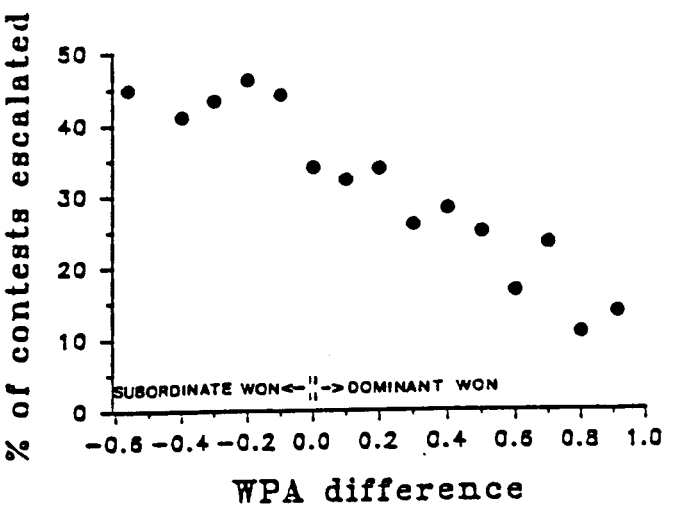


Fig.7.23. The percentage of Snow Bunting contests which were Fights, in relation to the difference in WPA between the Winner and Loser (WPA of Winner minus WPA Loser). *All points represent 50+ contests, and are the means for each 0.1 change along the x-axis, except the end points which were aggregated to ensure samples of more than 50 contests.*

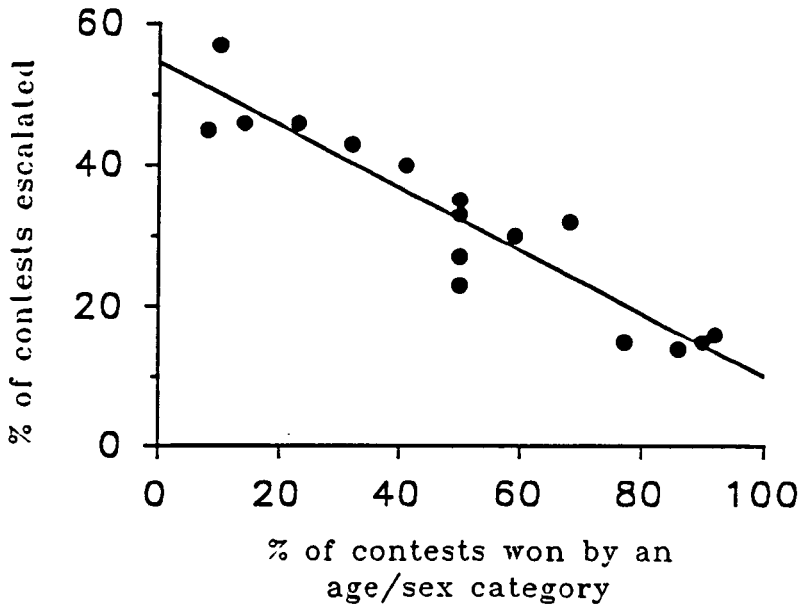


Fig.7.24. The percentage of contests between Snow Bunting age/sex categories that were escalated in relation to the percentage of contests won by one age/sex category over the other. *The percentage of contests escalated is calculated for those interactions won by the age/sex category in question, and so each pair of age/sex categories occurs twice (e.g. 46% of interactions won by adult females over adult males were escalated; the corresponding opposite figure for contests won by adult males over adult females was 14%).*

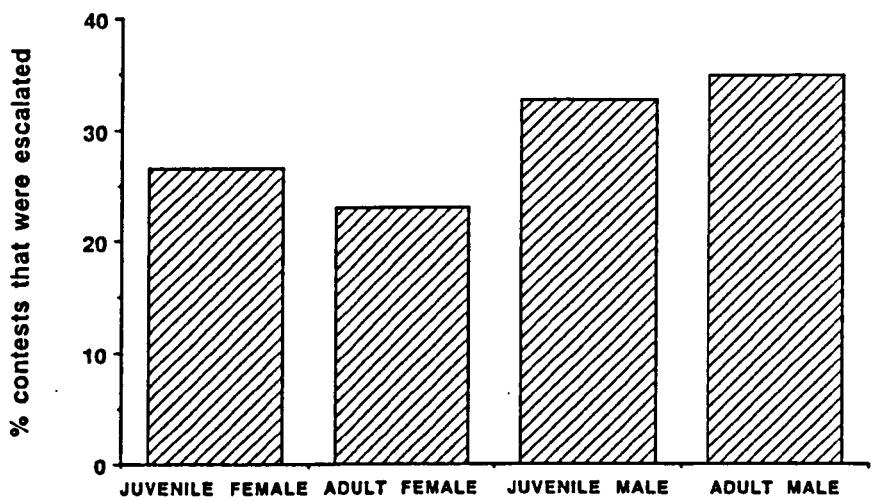


Fig.7.25. The percentage of contests between Snow Buntings of the same age/sex category that were escalated. *Sample sizes are (left to right) 94, 243, 300 & 4231 contests.*

Table 7.20. The percentage of contests escalated in relation to the size of the food patch and the size of flock of feeding Snow Buntings. *The sample size of contests is given in brackets. There was no evidence that either patch-size or flock-size affected the degree of escalation.*

	Average flock-size:			
	1.5-2.5	3.0-5.5	6+	Σ
Small patch	30 (10)	26 (39)	36 (80)	32 (129)
Large patch	50 (4)	43 (7)	18 (17)	29 (28)
Both patches	36 (14)	28 (46)	33 (97)	32 (157)

7.4 DISCUSSION

7.4.1 Social and environmental influences on aggression rates

Rates of aggression have often been observed to change with variation in temperature and food distribution, but the direction of these changes has not always been consistent. Pulliam *et al.* (1974) and Caraco (1979), for instance, found that rates of aggression were lower at cold temperatures in two species of juncos, while Barnard (1980b) observed higher aggression rates at lower temperatures in House Sparrows. Rates of aggression were higher in small patches in Dark-eyed Juncos (Balph 1977) yet lower in small patches in the closely related Yellow-eyed Junco (Caraco 1979). Although aggression increases more predictably with increasing flock-size (e.g. Caraco 1979, Barnard 1980a,b, Bekoff & Scott 1989) or flock density (e.g. Davies 1976, Balph 1977, Goss-Custard 1980, Ens & Goss-Custard 1984, Metcalfe & Furness 1987, Saino 1994), clearly the economics of aggression vary in different environmental circumstances.

In Snow Buntings, aggression at a patch of constant size was more frequent on cold days (after controlling for flock-size) or on days with more lying snow. The obvious correlation between snow-lie and low temperatures, and the slightly different importance put on them by different analyses (**Tables 7.2 & 7.3**), prevents me from separating their effects. Aggression may have been more frequent in Snow Buntings on these occasions because they were hungrier (as found in Dark-eyed Juncos by Ramenofsky *et al.* 1992, see also **8.3.3**), they expected future food limitations due to deteriorating conditions, or they had fewer feeding

options available on the surrounding ice- or snow-covered natural vegetation.

It has been shown in some species that aggressive behaviour can cause greater dispersion within flocks (Balph 1977, Vines 1980) or even limit flock size (Pearson 1989), although some species may be attracted to situations where rates of aggression are high (Kennedy & Gray 1994). My own data from small and large patches indicate that levels of aggression, for a given number of birds, were higher if birds were forced to feed on a smaller patch (i.e. flock density was higher, **Fig.7.3**). In the largest flocks, not only did birds compete for a feeding spot when they arrived at the patch, but they also maintained/suffered high levels of aggression throughout their feeding stint (**Fig.7.3**). Because the rate of aggression increased in dense flocks and snowy conditions, any costs associated with aggression would escalate when available food was distributed only amongst a few localised patches, even if these patches were rich and could provide for the needs of all birds present. In natural habitat, feeding patches would become increasingly localised as snow-depths increased. In such conditions, Snow Buntings usually arrived at the feeding patches in groups, fed for a few minutes and left as a group. If subordinate birds deferred feeding until the flock density on the patch had decreased, they risked getting little or no food (flock departure appeared to be initiated either through disturbance or restlessness among an increasing number of birds which had stopped feeding). They were therefore forced to experience high aggression levels to both remain with the flock *and* feed. Increasing rates of aggression may thus have been partly responsible for the decision of some birds, particularly subordinate females and inexperienced juveniles (see **5.3.5** & **9..3.2**), to leave Cairn Gorm in cold, snowy conditions (as predicted in the models of Gauthreaux 1978 and Pulliam & Caraco 1984).

7.4.2 Choice of opponent

Evidence for or against the exploitation of subordinates by dominant Snow Buntings was equivocal. Contests between dominant and subordinate adult males were commoner than expected (**Fig.7.15**), but there was no correlation between the rank of adult females or juvenile males and their adult male opponents. Nor did adult males of different competitive abilities differ in their likelihood of interacting against more dominant (juvenile male) or less dominant (female) age/sex categories (**7.3.4**). Females were not targeted at a significantly greater rate than males (**Fig.7.5**). This suggests that their lower proportion of contest initiations (as a proportion of all contests in which they were involved as resource possessors, **Fig.7.17**), was not due to a greater tendency to be attacked by males, but a lower tendency to start contests when already possessing a resource. Inexperienced birds, rather than the less competitive females, seemed to have reduced access to central feeding positions within flocks, although females fed somewhat later and in smaller groups than males (**6.3.4**).

In some situations it might pay dominants to preferentially displace the more subordinate individuals (e.g. when initially arriving at a food patch). In others it could be beneficial to tolerate them in order to exploit any rich sources of food that they find, or to use them as a shield from fellow dominants or predators

(Rohwer & Ewald 1981 - The Shepherds Hypothesis). Aggression may instead be targeted at fellow dominants in order to assert status or prevent infiltration of dominance hierarchies by cheats (Rohwer & Rohwer 1978 - The Social Control Hypothesis). Alternatively, contests between fellow dominants may be more frequent than expected if food sources are small and unable to accommodate all flock members simultaneously (e.g. Ketterson 1979a). Rohwer & Ewald (1981) appreciated the role that food dispersion played in determining whether contests were mainly between birds of similar or dissimilar competitive ability. Several studies have presented evidence for or against preferential like-versus-like fighting (e.g. Moller 1987a,b, Keys & Rothstein 1991, Slotow *et al.* 1993), but have only used one feeding regime and have not controlled for possible differences in spacing between dominants and subordinates. To my knowledge, only Theimer (1987) has provided evidence showing active choice of opponent. He found no difference in spacing between dominant, intermediate and subordinate members of Dark-eyed Junco triads, but dominant and intermediates interacted more frequently than expected, therefore indicating a role for social control in this species. In support of this, Jackson (1991), also using Dark-eyed Juncos triads, found that dominants were most likely to initiate the first contest, and that the intermediate-ranking individual was more likely to be the target than the subordinate bird. No study of opponent choice has controlled for whether or not the initiator already had access to a resource when attacking.

Active (non-random) choice of opponents is therefore difficult to demonstrate. Although there is some evidence suggesting exploitative competition in Cairn Gorm Snow Buntings, this may be a result of dominant birds selecting subordinate opponents to supplant when they arrive at a food patch, and/or being on average closer to subordinates than to other dominants (a 'shepherd' effect - Rohwer & Ewald 1981). As food patches were not always presented in a controlled manner I cannot, however, rule out that contests were more exploitative than the results suggest - on some days I presented small patches deliberately in order to encourage competition, but this may also have forced dominants to feed in closer proximity. A detailed study of opponent choice would require accurate data on spacing of individuals and feeding status prior to an attack from a variety of food presentation patterns. It was beyond the scope of the present work - sufficient control may only be possible in laboratory situations with smaller numbers of birds (e.g. Theimer 1987).

7.4.3 Costs and benefits of aggression

Irrespective of who wins an encounter, aggression is a costly behaviour. As well as the physical risk of injury during an encounter (reviewed by Huntingford & Turner 1987), increased levels of aggression are sometimes associated with hormonal changes indicative of stress (Schwabl *et al.* 1988) and have been shown to reduce foraging efficiency (Fleischer 1983), especially if food patches are small (Elgar 1987). To counteract these costs, contest initiators must perceive a probable net benefit from their attack. Active initiation of a contest should not occur if the chances and benefits of winning are not high enough to offset the risks and costs of losing *plus* the benefits of not fighting. Hence, many workers have reported high

success rates for contest initiators, e.g. Balph 1977 (>99%), Harrington & Groves 1977 ("virtually all"), Metcalfe & Furness 1987 (96-98%), Choudhury & Black 1991 (99.6%), Keys & Rothstein 1991 (96%).

Initiators also won the majority (82-92%) of contests in Snow Buntings, even if the initiator had lower resource holding potential than its Target (**Table 7.18**). Birds that won contests were more likely than losers to have continued access to the feeding site and to resume feeding quickly (**7.3.2**). Because birds were more likely to be involved in aggression when they first arrived at a patch (**7.3.1b**) and were more likely to initiate an encounter when they did not already have access to the contested resource (**7.3.5a**), involvement in aggression may often have been a prerequisite to feeding.

Most losers were birds that were approached when in possession of a resource (**7.3.5a**). They were usually still actively feeding when approached, and therefore, on average, probably lost some foraging time both during the interaction and as a consequence of having to move away afterwards. The costs of losing may have been minimised by moving away immediately, thereby avoiding physical contact. Although escalation may have increased the risk of injury or stress, it apparently did not reduce the probability that a contestant would still be present or feed within 5s (**7.3.2**). However, the effect of escalation may have been disguised if, for example, birds which moved away after a threat did so more readily (less benefits from future feeding) than birds which were prepared to escalate.

Unlike work done on some other small passerines (for example American Goldfinches, Popp 1987b; Siskins and Serins, Senar *et al.* 1989, 1992b; Silvereyes, Wilson 1994), I did not classify the initial behaviour of an approaching bird into a display type or as a 'threat' or 'attack'. This was because I could detect little sign of displays or cues from the attacking individual which the target could use to predict its motivation. Although subtle differences in the approaching bird's posture or speed of approach may have conveyed some information to the Target, there was certainly little evidence of more obvious displays used by other species (e.g. the 'Wingflap Displays' recorded by Popp 1987b, or 'Wing flutters', 'upright displays' and 'challenge calls' recorded by Wilson 1994). Perhaps the lack of a well-developed display of intent is associated with the Snow Bunting's diet. In the other species studied, during some parts of the year individuals depend to some extent on highly clumped food supplies (e.g. seed cones, seed heads or fruits), and may have developed a wide variety of displays as a result of the benefits of defending such food sources. In contrast, Snow Buntings largely feed on less clumped seed supplies: seeds of grasses, often after they have fallen to the ground. The benefits of resource defence may not have merited the evolution of a complicated display system for such scant rewards. Moreover, nearly three-quarters of contests were settled without any retaliation from the target (**7.3.5c**) so the likelihood of winning by just approaching an opponent was high. Indeed the likelihood that a contest would become escalated appeared to depend more on the behaviour of the Target than the Attacker. Hence, encounters which became escalated were less likely to be won by an Attacker than those which were not. Both Popp (1987b) and Senar *et al.* (1992b) showed that although highly intimidatory displays or attacks were more effective (in terms of winning the

contest), they also had greater risks (higher probability of involving physical contact). Given that simple approaches were often effective in Snow Buntings, irrespective of dominance status, there may have been little need to begin contests with a more intimidatory yet risky behaviour, especially on the rather rich patches that I provided. Moreover, time lost performing a more sophisticated and potentially riskier display could perhaps not be justified under natural conditions when the rewards of winning would normally be small (e.g. in snow-free conditions access to one or a few small seeds). Even under my feeding regime the benefits of winning may not have been large: two-thirds of losers had resumed feeding elsewhere a few seconds later, whilst some of the defeated birds, as a result of satiation, may not have *wanted* to continue feeding (see later).

On a few occasions during deep snow, I provided tiny (up to 25cm²) patches, or allowed flocks to fight over small (monopolisable) pits in the snow to a buried bait source below. Unfortunately, these observations were not separated from the others (because at these times recording of aggression was not usually given my highest priority), but it did appear on these occasions that some individuals monopolized the patches for long periods and were not likely to move when approached. My impression was that individuals monopolizing the tiny patches were usually birds of high dominance status, and that they were more overtly aggressive at these times (for example, a higher frequency of attacking nearby birds even when these were not feeding, even more so than when feeding in large dense flocks). These tiny patches could have been more valuable (because during deep snow there were few other feeding options) and hence worth defending, and the intentions of the monopolizing birds to hold onto their patches may have been conveyed by the frequency of these unsolicited attacks (rather than by a more sophisticated display).

The probability that a bird would capitulate immediately decreased as its resource holding potential, relative to the initiator, increased (**Fig.7.20**), perhaps because dominants, as a result of a relatively lower risk of injury in a fight with a subordinate, could afford to 'test the resolve' of the subordinate initiator. The fact that subordinate initiators still won a large proportion (45%) of contests when rebuffed physically, may indicate that their decision to attack was not always a bluff, but based on an accurate assessment of their target's ability and willingness to fight back. As expected on theoretical grounds (Parker 1974), encounters were most likely to escalate into Long Fights when the contestants were most evenly matched.

It is therefore possible that subordinates could displace dominant Target-Possessors relatively easily because they waited for dominants to satisfy their foraging needs to some extent before approaching them. The benefits to dominants of further feeding decrease as reserves build up (McNamara & Houston 1986), while the benefits of deferral to a subordinate (avoiding injury and perhaps helping to maintain flock cohesion - Senar *et al.* 1989) remain constant. At some point, as feeding progresses, the fitness benefits of deferring to a subordinate opponent will outweigh those of further feeding. In support of this, females fed significantly later in feeding bouts than males (**6.3.4b**). This may also explain some of the age/sex differences in response to winning or losing a contest (**7.3.2**): losing females were more likely to continue

feeding (i.e. peck within 5s) than losing males (which may have been relatively more satiated); the greater tendency for naive winners (in comparison to experienced winners) and juvenile losers (in comparison to adult losers) to stay On the patch may better reflect greater hunger levels, or expectation of hunger in juvenile or naive birds (because these birds had lower feeding rates/efficiencies; **Chapter 6**).

Initiating a contest when already holding a resource is less easily explained. Only about 16% of contests were started in this way, and there was no consistent change in its frequency with the relative resource holding power of the initiator (**Fig.7.18**). Instead, initiation when in possession of a resource was more frequently associated with juvenile males than expected. Despite the larger success rate (99%; even 94-96% in subordinates) of this strategy compared to initiation when intruding (**Fig.7.16**; similar results obtained by Senar *et al.* 1989), initiation when in possession will impose a cost of fighting and a risk of losing. There may, of course, be some benefit from striking first, to prevent a future usurption. Also, since juvenile males were often of high dominance status and may have been most likely to try to monopolize very small food patches, unsolicited attacks may have been used more frequently by these birds to display their intention to defend the tiny patches (see discussion above). Alternatively, however, inappropriate initiation of aggressive interactions may be associated with the social inexperience of juveniles. Groves (1978) suggested that such a phenomenon might explain the high rates of aggression shown by adult Turnstones to juveniles. Likewise, Goss-Custard & Durell (1987) proposed that juvenile Oystercatchers might take several months before becoming proficient in targeting suitable opponents. Therefore, unnecessary or inefficient involvement in aggression may also be a more common feature of juvenile than adult Snow Bunting behaviour.

7.4.4 Correlates of dominance

Differences between the sexes are perhaps the most widely reported sources of variation in dominance. Males are usually dominant to females (references in Gauthreaux 1978; also Arcese & Smith 1985, Waite 1987, Weidenmann & Rabenold 1987, Enoksson 1988, Hogstad 1988b, Wechsler 1988, Bekoff & Scott 1989, Grubb 1989, Hepp 1989, Komers 1989, Piper & Wiley 1989, Richner 1989, Ekman 1990, Wagner & Gauthreaux 1990, Choudhury & Black 1991, Keys & Rothstein 1991), except in some species with reversed sexual size dimorphism (e.g. Snyder & Wiley 1976). One notable exception is the House Finch, where the larger males commonly defer to females in winter (Brown & Brown 1988), possibly to maintain year-round pair-bonds. Snow Buntings conform to the general pattern, with males, the larger sex by 2-9% in linear body dimensions (Banks *et al.* 1989), winning 80-90% of encounters between the sexes (**Tables 7.4 & 7.6**).

Sex differences in dominance are often associated with size differences between the sexes. Several avian studies have shown that size can be an important correlate of dominance by looking at the effect of size on dominance within genders (e.g. Searcy 1979, Jackson *et al.* 1988, Richner 1989, Koivula *et al.* 1993, Lemel

& Wallin 1993). Others have found no association between size and dominance (e.g. Arcese & Smith 1985, Eden 1987, Weatherhead & Teather 1987, Weidenmann & Rabenold 1987, Kikkawa 1980, Piper & Wiley 1989, Post 1992). Similarly in Snow Buntings there was no suggestion that, within either sex category, dominance was related to wing-length (**7.3.3f**), suggesting that size differences may not be the main reason why males have a dominance advantage over females. Instead, because males are responsible for maintaining territories in Snow Buntings (Tinbergen 1939), they may have developed a greater degree of innate aggressiveness which persists at other times of the year. Although Snow Bunting age/sex categories did not differ in their rates of becoming involved in aggression (**7.3.1b**), adult females initiated encounters at lower rates than the other age/sex categories. Watson (1970), Wechsler (1988) and Komers (1989) also provide examples where females fight less frequently, on average, than males. Moreover, relative aggressiveness rather than relative dominance appears to affect contest intensity: after controlling for opponent-type and hence rank (by considering only contests between birds of the same age/sex category, **Fig.7.25**), contests between females were less likely to escalate than those between males.

During this study, I saw no evidence of territorial behaviour (i.e. defence of an exclusive space) in winter immigrant Snow Buntings, or in local breeders before March (when the future breeding territory may be proclaimed and defended part of the time - unpubl. obs.). Nor was there any indication that an individual's relative dominance depended on its location (**Table 7.13**), despite a test for this over much larger distances (>600m versus <200m) than those reported in studies of species which *do* exhibit site-related dominance (Wechsler 1988, Piper & Wiley 1989, Oberski & Wilson 1991). Furthermore, although my 'resident breeders' were not strictly resident in the non-breeding season, but merely spending winter in relatively close proximity to their breeding territories (mostly less than 10km from summer territories, compared to greater than 1000km to the territories of winter immigrants), they did not have a dominance advantage over winter immigrants (**7.3.3g**). This contrasts with studies of wintering Field Sparrows (Fretwell 1968) and Dark-eyed Juncos (Wiedenmann & Rabenold 1987).

Although not always taking into account the effects of prior residence at a site (see later), many avian studies have shown that adults are dominant to birds in their first year of life (e.g. Smith 1976, Groves 1978, Rohwer *et al.* 1981, Arcese & Smith 1985, Weatherhead & Teather 1987, Hogstad 1988b, Schwabl *et al.* 1988, Bekoff & Scott 1989, Black & Owen 1989, Catterall *et al.* 1989, Piper & Wiley 1989, Richner 1989, Wagner & Gauthreaux 1990, Dearborn & Wiley 1993). Post (1992) found that the dominance of Boat-tailed Grackles continued to increase as they got older. In contrast, aviary studies of Song Sparrows and Great Tits failed to find age effects on dominance (Wagner & Gauthreaux 1990, Lemel & Wallin 1993). One of the most contradictory results of my work, however, was that within Snow Bunting sex categories, dominance correlated *negatively* with age (**7.3.3a**). This result was even present *within* individuals, although there was no further decline in dominance after an individual's second winter (**7.3.3c**). Furthermore, in males (there was insufficient data for females), juveniles were still more likely to dominate adults than vice versa after controlling for an individual's role within a contest, and were able to win

encounters more easily (with less need to resort to physical contact; **2.3.5d**).

Studies where first-year birds have been shown to dominate adults are mostly restricted to species where kin might benefit (e.g. Pinon Jays, Balda & Balda 1978; Mexican Jays, Barkan *et al.* 1986), or where adults and juveniles lead very different lifestyles (Magpies - Dhindsa *et al.* 1989, Komers 1989, Komers & Komers 1992). Neither of these explanations could explain the observed pattern in Snow Buntings. Observations of local breeding Snow Buntings showed that fledged broods divided between the two parents soon after fledging and that independence from the parents occurred approximately two weeks later. Thereafter, parents and young were not known to associate together (unpubl. obs.), although there did not appear to be any division of age categories amongst separate wintering flocks. Harrington & Groves (1977) suggested that juvenile Semipalmated Sandpipers initiated more interactions than adults (and were hence dominant to adults) because they were "less efficient....in catching prey and therefore had a higher threshold for lowering aggression". In my study, although juvenile Snow Buntings may have been less efficient than adults, they retained their dominance advantage even in severe weather conditions, and even after controlling for who initiated the encounter. In the only other study that I am aware of which reported a situation in which juveniles dominated adults (Cristol *et al.* 1990), caged juvenile Dark-eyed Juncos were given a prior residence advantage. However, when individuals were introduced to cages at the same time, or under natural field conditions, the relationship was reversed in this species (Ketterson 1979a, Rogers *et al.* 1989, Cristol *et al.* 1990), and hence Cristol *et al.* concluded that age and prior residence were additive *positive* effects on dominance status.

Was my result associated with some methodological or sampling nuance which other studies have avoided? This study was based on the same technique to measure dominance as the vast majority of other published avian studies (see **7.1**), i.e. the supplanting of one bird by another during an aggressive interaction. Contests were discrete events, rarely had to be scored as draws (**Table 7.1**), and usually had clear and unambiguous winners. Therefore field methods appeared to be similar to other studies. Perhaps the statistical treatment of the data was inappropriate. I do not believe this to be the case, however, because on average juveniles consistently appeared to be dominant to adults at three increasingly restrictive levels of analysis (all interactions between age categories, all dyads between age categories, and individual dyadic success against other age categories; **7.3.3a, 7.3.3c**). Furthermore, for the small sample of individuals where dominance could be measured using perhaps the most stringent technique, namely by constructing a dominance hierarchy, dominance rank was closely correlated to individual dyadic success (win proportion when adult; **7.3.3b**). Few other field studies which include such large numbers of individuals test the reliability of their results to such an extent. Many are content to trust that the overall result of interactions between birds of different categories reflects relative dominance. Therefore it seems reasonable to conclude that the relative dominance of juveniles over adults did not occur as a result of inappropriate field or statistical techniques.

Perhaps, however, we are too quick to refer to the tendency of an individual (or group of individuals) to win aggressive encounters with others as 'dominance'. In certain situations, for example if the best individuals feed first before being displaced by hungrier but less capable individuals, subordinates may win *more* contests than intrinsically dominant individuals. Hopefully, researchers would recognise such situations and report an appropriate measure of dominance. Although it was not possible for me to look at variation in the proportion of contests won by juveniles at different stages of the flock's feeding bout, juvenile males did not appear to 'wait' for adults to feed before feeding themselves (**Fig.6.8**). The tendency for juveniles to be found in more peripheral feeding positions and to move off the central feeding arena (**6.3.4c,d**) may be more attributable to naivety than subordinance. I did, however, test for several other possible situational factors which may have influenced the outcome of contests (weather conditions, role and contest escalation), but still found that juveniles consistently won more contests than adults.

Similarly, dominance may be unjustifiably attributed to some individuals, not because they are more able competitors, but because they *initiate* contests and as noted earlier, individuals which initiate interactions often have a high probability of winning. Initiation of aggression may reflect an individual's need to win rather than its actual dominance. In this study, and in some others (e.g. Senar *et al.* 1989) deferrals by dominants to subordinate birds were frequent. Goss-Custard & Durell (1987) showed that the agonistic success of juvenile Oystercatchers was high early in the winter when they were more likely to attack other birds, but *declined* throughout the winter as their contest initiation rates dropped. Presumably these juveniles did not become intrinsically less dominant during this period, only less aggressive as their own feeding expertise increased (Goss-Custard & Durell 1987). Perhaps the results of Harrington & Groves (1977) occurred in a similar context: juvenile Semipalmated Sandpipers won interactions simply because they initiated them. Again, however, this argument does not seem to explain the greater success of juvenile versus adult Snow Buntings because agonistic success was greater in the former irrespective of their role in the contest.

A priori, I could suggest three possible ways in which juvenile Snow Buntings might be seen to have a dominance advantage over adults. Firstly, juveniles that were able to remain on Cairn Gorm for long periods during their first winter may have been more competitive than average juveniles of the same sex. In this case we might expect that birds which became established on Cairn Gorm only when adult would be *less* competitive than average adults (which would comprise at least some birds which had become established as juveniles - see **Fig.9.5**). However, this was ruled out because naive adult Snow Buntings won *more* encounters than experienced adults against given age/sex categories of opponents (**Table 7.7**).

Secondly, birds that survive and return to Cairn Gorm in their second winter may be of lower dominance status than birds which do not. This may be because non-returners are more likely to die between their first and second winters, or because these birds survive but choose to winter elsewhere (by implication, further north or in better habitats, see Gauthreaux 1978 and **4.4**). Juvenile males which returned to Cairn Gorm in

subsequent winters had marginally, but not significantly, lower agonistic success (as measured by WPAs) than juvenile males which did not return (**9.3.4**). There was therefore no evidence of differential losses (through mortality or dispersal) between dominance ranks, although individuals were known to change sites between years (**5.3.6**). Alternatively, of course, it may have been the adults which showed differential return rates between winters in relation to dominance. Considering that it is unusual for birds to be more likely to change their patterns of site use when adult as opposed to when young (e.g. Townshend 1985), it is not surprising that again there was no support for this (**9.3.4**).

The third possibility is that individual birds were actually more likely to win a contest against a given standard of opponent when they were a juvenile than later in life. The first two suggestions differ from this third because they do not require that the dominance status of an individual changes during its lifetime. Under the first two suggestions, it could, in some circumstances, even be possible that individuals *increased* in dominance with age. However, my finding that dominance decreases with age *within individuals* (**7.3.3c**) clearly supports my third suggestion.

Possibly juveniles place more value on contested resources than adults, and hence are prepared to risk more, or spend more energy, to acquire them. A number of studies have shown that manipulating the value of a resource for one competitor, while keeping its value constant for the other, results in a higher success rate for the manipulated bird (Popp 1987a, Andersson & Ahlund 1991, Cristol 1992, Lemel & Wallin 1993). In this study I expected that on occasions when the resource value was especially high, such as during bad weather or as indicated by contest escalation, the contestant with the higher resource holding potential (reportedly adults in most studies) would be more likely to win. However, bad weather appeared to have little effect on the outcome of contests (**Fig.7.14**), and juvenile males continued to dominate adult males even when contests escalated into fights (**7.3.5d**). Neither was there much evidence that bad weather or restriction of access to food caused a greater proportion of contests to escalate (**7.3.5e**). It is still possible that the maximum agonistic efforts of adults may be on a par with or exceed those of juveniles, but that the conditions required to produce maximum effort were not recognised, or infrequently arose, in this study. Instead, worsening conditions may have caused the relative value of a resource to increase for both contestants equally, maintaining the difference between them in the effort they were prepared to expend in a contest (and not reaching the maximum effort that a juvenile could expend), and hence perpetuating the apparent dominance of juveniles over adults.

Additionally, adults may be more adept at finding food, and hence represent more valuable 'victims' of aggression. Goss-Custard & Durell (1987) used this idea to explain why juvenile Oystercatchers were more likely to attempt to steal food from adults than fellow juveniles. Although food stealing has not been observed in Snow Buntings, juveniles may benefit from stealing *feeding sites* from adults. There may have been little benefit of supplanting adults at the uniform bait patches which I provided, but considerable value in more heterogenous natural habitats. Habituation with winning encounters has been shown to reverse

expected dominance relationships (e.g. Baptista *et al.* 1987). Juveniles may therefore have continued to supplant adults at my feeding sites because they had become habituated to such behaviour elsewhere.

As agonistic success did not appear to continue to decline as individuals aged (**Fig.7.13**), it is unlikely that the observed reduction between an individual's first and second winters was due to some physical inability to win contests (e.g. accumulation of weaknesses and injuries with time). It is possible that if contests were held under more controlled circumstances, or if the contested resource value was increased, adults might be more successful than juveniles. Neither could be shown in this study, despite considerable efforts to gather detailed data under a variety of environmental conditions. Nor could I find any seasonal reduction in juvenile success (**7.3.3a**), as associated with increasing foraging efficiency in Oystercatchers (Goss-Custard & Durell 1987). Juvenile dominance in winter feeding squabbles therefore appears to be a deeply engrained characteristic of the population of Snow Buntings studied here. Indeed, the lack of any seasonal reduction in juvenile agonistic success, despite probable increases in foraging efficiency (**6.3.2c**), suggests that persistent hormonal or physiological processes may be involved.

However, I think it is important to restrict the extent to which juveniles can be claimed to dominate adults. Smith (1994), for example, found that adult males, some of which were from the observed wintering population, were more likely to find mates in the breeding season than juvenile males. Although this may have reflected female choice rather than any aspect of relative male dominance, it is also possible that this is one circumstance where adult males assert a reliable competitive advantage for an undoubtedly important resource.

In tandem with the dominance of juveniles over adults, it was perhaps less surprising to find that experienced Snow Buntings were *less* likely to win interactions (after controlling for age and sex) than birds with less site experience (**Table 7.7**). However, the result is still important because prior residence or experience at a site or situation generally *enhances* dominance status. In field studies, prior experience at a site increased the probability of winning an encounter in Dark-eyed Juncos and Siskins (Ketterson 1979a, Senar *et al.* 1990b, Senar & Metcalfe 1988) but had no effect in White-throated Sparrows (Piper & Wiley 1989). It also facilitated the acquisition of high dominance ranks in non-breeding Marsh Tits and Magpies (Eden 1987, Nilsson 1989). In captive birds, even the introduction of one individual to a cage a few days prior to an opponent can increase its chances of success in interactions (e.g. Balph 1977, Balph 1979, Dhindsa *et al.* 1989, Cristol *et al.* 1990, Holberton *et al.* 1990, Wiley 1990, Koivula *et al.* 1993) and this advantage increases as the length of prior residence is increased (Dearborn & Wiley 1993). It may also be sufficient to overcome previous dominance relationships (Yasukawa & Bick 1983). I am not aware of any previous study which has shown that naive birds have *more* success in interactions than birds with greater site experience.

There was little evidence, unlike in inexperienced juveniles, that inexperienced adult Snow Buntings

became less dominant when they returned in future winters (**Fig.7.12**), but the sample was small and the difference in relative rank between experience groups was less than that observed between age groups. Perhaps, however, the greater probabilities of winning an encounter when young or unfamiliar with a site are linked. Lack of knowledge about where or when patches of food are likely to become available, may make inexperienced birds more likely to initiate and/or escalate encounters over a current food source. The magnitude of the difference in foraging efficiency (**6.3**), and the greater knowledge of adults versus juveniles about alternative feeding sites, or what types of food or patches are exploitable in particular conditions, may explain the greater effect of age, relative to experience, on dominance.

7.4.5 Ecological implications

The large intersexual dominance advantage enjoyed by males may underpin differences between the sexes in site selection and site fidelity (**Chapters 4, 5 & 9**). Females had similar feeding rates to males in small flocks, but could not maintain these in large, dense flocks (**6.3**). Competitive situations like these may be brought on by snowfalls, causing food patches to become smaller and more localised. Hence, the best option for many females would be to select sites where snow is less frequent and/or to leave sites when snow falls or competition becomes too severe.

The somewhat smaller differences in dominance noted between age and experience categories were opposite to that expected if inferior competitors were being excluded from high altitude sites. Juveniles and inexperienced birds were dominant, yet the former were less well-represented than expected at the high quality (see **4.4**) high altitude sites (**4.3**). Both were more likely to leave these sites when snow fell (**5.3.5, 9.3.2**). Other correlates of age and site experience, particularly foraging efficiency (**Chapter 6**), may thus be far more important influences on site selection and site fidelity.

Chapter 8: ENERGY RESERVES

8.1 INTRODUCTION

Food intake in most birds is a day to day necessity. Individuals build up a reserve of metabolisable energy to sustain them when circumstances prevent feeding (e.g. periods of darkness, bad weather, acute predation risk, illness, migration, etc.). This energy reserve usually takes the form of stored body fat, and a build-up of stored fat is often reflected, and measured, by increased body-mass (Blem 1990). Generally, the greater a bird's energy reserves, the lower the risk of future starvation. But there are also considerable costs of building-up and maintaining higher energy reserves, particularly in terms of increased predation risk, either because individuals risk exposure to predators for longer whilst feeding, or because their ability to successfully evade the attack of a predator is reduced due to their extra mass (reviewed by Witter & Cuthill 1993, demonstrated by Witter *et al.* 1994).

Theoretical work therefore predicts that birds will not increase energy reserves indefinitely, but instead will endeavour to maintain an optimal amount of energy reserves in which total mortality (largely the sum of starvation and predation) is minimised (Lima 1986, McNamara & Houston 1990, Houston & McNamara 1993). This optimal amount of energy reserves will not be constant, but will vary in accordance with perceived future food availability and predation risk (e.g. Witter *et al.* 1994). For some species, food availability is most limiting in mid-winter when daylight hours are shortest and weather conditions are often most severe. They counteract the increased risk of starvation during these periods by attempting to increase the amounts of stored fat at their disposal. 'True winter fattening', as defined by Lehikoinen (1987), involves the build-up not only of greater fat reserves to ensure survival over the longer, colder nights, but also of additional reserves, most obviously present at dawn, which facilitate survival over longer periods if food availability is reduced. Dynamic models (Houston & McNamara 1993) have further formalised this phenomenon, but more importantly, it has now been established empirically on several occasions (Lehikoinen 1987, Haftorn 1989, Rogers & Rogers 1990, Waite 1992). For similar reasons, increased fat reserves are also associated with wintering at higher latitudes (e.g. King & Farner 1966, Nolan & Ketterson 1983, Hotker 1989, Cuadrado *et al.* 1989, Summers *et al.* 1990, Castro *et al.* 1992), colder temperatures (predicted by Lima 1986, McNamara & Houston 1990; evidenced by King & Farner 1966, Nolan & Ketterson 1983, Blem & Shelor 1986, Jenni & Jenni-Eiermann 1987, Ekman & Hake 1990), windier conditions (Waite 1992, Witter *et al.* 1994), snowier conditions (Nolan & Ketterson 1983, Waite 1992), long-term trends of worsening weather conditions (Dawson & Marsh 1986, Peach *et al.* 1992), greater variability in food availability (Rogers 1987, Ekman & Hake 1990) or reduced predation risk (Jenni 1993, Witter *et al.* 1994).

Only rarely are these additional reserves called upon to prevent starvation, at least at the population level (e.g. Bennett & Bolan 1978, Dugan *et al.* 1981, Davidson & Evans 1982, Rogers *et al.* 1991, Fox *et al.*

1992). Indeed, theoretical work predicts that mortality due to starvation will often be much lower than predation, and that rates of starvation in a population may be *higher* when mean reserve levels show an increase (Houston & McNamara 1993). This is because *individual* birds may be more likely to starve at these times due to unpredictable variations in feeding conditions. As feeding or weather conditions deteriorate, individuals or populations may elect to move away from a site well before starvation is imminent (e.g. Evans 1981, Pattenden & Boag 1989), even though they must use valuable energy in doing so, and risk not finding better conditions elsewhere.

Within populations, individuals may vary in the amount of energy reserves they store. Theoretically, for a given proportion of stored body fat, larger individuals should survive for longer periods without food (Kendeigh 1969, Calder 1974), although if limited food is available the situation may be reversed (McNab 1971). Factors such as dominance and experience may therefore be far more important than size in determining an individual's optimum stored energy reserves. Older birds usually have greater fat stores or mass levels than juveniles (e.g. Kikkawa 1980, Dougall & Appleton 1989, Summers *et al.* 1990), but not always (e.g. Coulson *et al.* 1983, Baldassarre *et al.* 1986). Dominant birds are also sometimes heavier (Kikkawa 1980, Piper & Wiley 1990b).

If birds of higher quality (older or dominant) are usually also heavier, studies failing to find evidence for differential survival of heavier birds are surprisingly common (e.g. no effect of mass on survival reported by Kikkawa 1980, Krementz *et al.* 1989, Piper & Wiley 1990b). However, a few studies have indicated a fitness advantage associated with energy reserves. For example, Rogers *et al.* (1991) found that Fox Sparrows, which carried more fat than Song Sparrows, survived better through a long and severe spell of bad weather. In addition, Lehikoinen (1986) suggested that heavy juvenile Great Tits survived best in cold winters, but those with intermediate masses were favoured in milder winters. Adult or experienced birds might, indeed, be expected to maintain *lower* optimal levels of energy reserves than naive or young individuals because they have more knowledge about how or where to find food when conditions deteriorate, and hence a more predictable food supply. Similarly dominants may retain lower fat reserves than subordinates if they have priority of access to food in bad conditions. Ekman & Lilliendahl (1993) proposed that this explained their observation that dominant Willow Tit flock members were lighter than subordinates. However, behavioural differences between birds of different status may modify or reverse these trends - if dominants also feed or roost in safer sites, then they can afford to maintain greater fat reserves (reviewed by Witter & Cuthill 1993; also Jenni 1993). Still further complications arise because unless the study populations are known to be able to feed *ad libitum*, it is always possible that stored energy reserves are not optimal when measured, and that the mass of old, experienced or dominant birds may be greater because they are closer to the optimum (e.g. Wagner & Gauthreaux 1990 found greater rates of mass loss in subordinate versus dominant Song and White-throated Sparrows).

Winter energy reserves, as measured by body-mass, have been studied previously in Snow Buntings by

Vincent & Bedard (1976) and Banks *et al.* (1989). The former studied mainly captive birds and found correlations between mass and long-term average temperatures, day-length, actual snow-cover and long-term snow-cover. However, the direction of the correlations was reversed depending on the social conditions the birds were kept under (singles, pairs, tetrads or groups of 12), and it was difficult to interpret any overall pattern. Banks *et al.* (1989) presented data indicating that masses of wild-caught Snow Buntings remained fairly constant throughout the winter period, before increasing rapidly before migration in March. Another relevant study is that of Heiniger (1991) who reported that the morphologically and ecologically similar Snow Finch showed a late January peak in body-mass.

In my study, it was obvious from an early date that birds which were long-term winter residents on the ski areas were caught less frequently than expected (see **5.3.2**). Although it was possible to describe mass patterns of birds at these sites from masses of caught birds, and it was possible to compare data between sites, these data were inevitably biased towards transient individuals. The number of birds present, and the weather conditions prevailing in the first four winters suggested that turnover of birds was large and mainly in response to weather conditions (see **5.3.4, 5.3.5**). Perhaps birds built up energy reserves between bouts of snow, lost them differentially during snow, then left the upland sites as reserves became depleted. In theory, weighings before a snow-bout could establish how optimum mass levels were related to bird quality, whilst patterns of mass gain/loss within individuals during snow-bouts could show how different types of individual would cope with the conditions, and possibly relate to decisions to leave the site. It was therefore decided to attempt to weigh birds as frequently as possible using electronic perch balances to which, I hoped, they were oblivious. However, weather patterns and the number and diversity of Snow Buntings using Cairn Gorm during 1991/92 and 1992/93 largely limited these ideals. Nevertheless, an analysis of the mass data is presented in this chapter, and some interpretation of the results, albeit *post hoc*, is attempted.

8.2 METHODS

Snow Buntings were weighed either when captured, or when attracted to feed on top of electronic weighing balances. The former method allowed a large sample of birds to be measured, but trapshyness (see **5.3.2**) limited the number of times that individuals could be captured (maximum = 7 captures), preventing me from establishing patterns *within* individuals. The electronic balances were introduced in late February 1991 to try to solve this problem.

8.2.1 The trapped sample

I trapped Snow Buntings on the three ski areas in each of the six winters from 1987/88 to 1992/93, and at the two upland farmland sites (The Cabrach and Corgarff) in January to March 1988. Additional data were available from birds trapped on the coast by Grampian Ringing Group (as in **Chapter 4** - Balmedie,

Newburgh and Rattray) in winters 1987/88 and 1988/89.

During handling, I weighed almost all birds to the nearest 0.1g on Salter or Pesola balances. Visible fat deposits in the furcular (tracheal) region were also estimated on most birds using a six-point scale modified slightly from that of Helms & Drury (1960): 0 = no visible fat in the furcular pit; 1 = traces of fat, but not completely covering the base of the furcular pit; 2 = fat filling the base of the furcular pit to the clavicles, but furcular region still appearing concave; 3 = as 2, but fat level with top of furcular pit; 4 = furcular pit conspicuously mounded, but no fat beyond the clavicles; 5 = fat visible outside and over the furcular pit.

The relationship between energy reserves and body-mass in a sample of birds is often enhanced if some linear body measure is included to control for individual variation in body-size (e.g. Slagsvold 1982, Blem 1990). To minimise handling time, the only linear measurement I took from Snow Buntings was their wing-length (**3.2**). This measurement shows little within-individual variation over the course of a winter, but increases between an individual's first and second winters (see **3.3.3**). This increase may be a result of ecological or nutritional limitations on fledglings (**3.1**), rather than overall body growth between an individual's first and second years. Other skeletal measurements in passerines indicate that body growth is completed within the first few months of life (Slagsvold 1982, Smith *et al.* 1986). I therefore assumed in this chapter, that juvenile birds caught in winter *were* fully grown, but that their wing-length underestimated their body-size. Wing-length was therefore adjusted to that of adults by adding 1.1mm to the wing-length of juvenile females and 1.7mm to that of juvenile males prior to analysis (amounts derived from the average wing-length increases shown by individuals or sexes in first versus second or subsequent winters, as measured in **3.3.3**).

Mass loss between capture and weighing was a potential problem, depending on how much it varied in relation to how long the bird was held. The capture technique (discrete catches of up to 68 birds, rather than a constant turnover of new birds) inevitably meant that there were delays between capture and the time each bird was weighed (mostly 30-90 minutes). I noted capture time of all catches, but not the length of time that each bird was held prior to measurement of its mass. Hence mass loss during holding, as a result of respiration or defecation, could not be calibrated. To assess the possible impact of mass loss on my results, I present data on mass loss shown by two catches of birds weighed twice during the time they were confined.

I investigated diurnal and seasonal variation in body-mass by including TIME (time of day when birds were caught, to the nearest 15 minutes), DAY (days from 1st October, excluding March and April when migration fattening occurred) and DAY^2 (square of DAY), as well as body-size related variables (SEX and WING-LENGTH), in stepwise multiple regression analyses on the dependent variable body-mass. I subsequently used the MASS RESIDUALs from these multiple regressions to look for variation in body-mass associated with changes in weather conditions, age (within sex category, since SEX was

controlled for in the original multiple regressions), site experience or dominance.

As there was significant variation associated with sex, wing-length, time of day and season (**8.3.3**), it was essential to control for these variables prior to some analyses. To accomplish this I used the parameters established in the above multiple regressions (see **Table 8.1**), unless otherwise stated. Time of day and season were usually standardised to values appropriate for particular analyses (e.g. dawn, noon, mid-December, etc.). However, the influences of gender and body-size on body-mass were usually controlled simultaneously by standardising body-mass by an amount expected if the bird had been an **average-sized male** (defined throughout this chapter as a male with a wing-length of 113mm, see **Table 3.3**).

Within catches, body-masses may have deviated in unison from that expected (after correcting for diurnal, seasonal or weather-related variation) because of unmeasured catch-related variables (e.g. disturbance, amount of bait eaten before the catch was made, expectation of good/bad feeding conditions to come, etc.). Hence, within catches, body-masses were not independent. I therefore selected catches of 10 birds or more, and calculated the mean body-mass of birds in the catch, standardising each bird's mass to that expected if it was an average-sized male. An individual's MASS DEVIATION was then the difference between its standardised mass and the mean standardised mass of the whole catch. This variable removed between-catch variation (as a result of diurnal, seasonal or any other unmeasured factors), but retained between-individual variation. I also calculated a FAT DEVIATION for each individual in the same way (although there was no need to standardise to a particular sex or wing-length). FAT DEVIATION, although somewhat more peaked than a normal distribution due to the limited range of the fat scoring system, was useful because it allowed comparisons of fat reserves *between the sexes* (unlike MASS RESIDUAL and MASS DEVIATION, where sex and size were controlled for in the initial multiple regressions). Subsequently I examined the effects of age, experience and dominance on MASS DEVIATION and FAT DEVIATION, and the affect of sex on the latter, and looked for interactive influences of weather variables.

8.2.2 Electronic balance data

My electronic balances, supplied by Vagspecialisten, Sweden, consisted of two load cells connected by c30m of cable to a remote digital read-out unit. During March 1991, and winters 1991/92 and 1992/93, I set out the load cells at CIFS next to the baited feeding area (see **6.2**). Snow Buntings were attracted on top of a 15cm x 15cm plastic platform placed on top of each load cell by sprinkling this with peanut granules. The birds appeared to prefer peanut granules to pinhead oatmeal, and therefore on most flock visits some birds were attracted to the balances, rather than to oatmeal on the larger feeding area. Up to three (occasionally 4-5) Snow Buntings could feed simultaneously on each platform, although this was often limited by aggressive behaviour.

The electronic balances were accurate to 0.1g under ideal conditions, but wind or movement of the feeding birds frequently limited this accuracy. Both load cells were connected to the same read-out unit, and although only one load-cell would register at a time, a manual switch connected to the read-out unit enabled me to choose which load cell to take readings from. When switched on, the chosen load cell automatically zeroed. Switching to the other unit gave a mass relative to this; any movement of birds on or off the balances then gave positive or negative mass readings respectively. Although it was possible to have the mass reading 'freeze' when a constant weight was attained (i.e. in theory, a stationary bird), this was not always reliable (e.g. the reading could freeze during a wind gust of constant strength, thus giving an inaccurate reading). Therefore, I let the read-out reading 'float' continuously and attempted to take an average reading by eye, registered on to a dictaphone - this also allowed a succession of mass readings to be taken as different individuals jumped onto and off the balances.

Snow Buntings appeared nervous of perspex wind baffles placed within 10-20cm of the balance tops, but they more readily fed next to a permanent wooden embankment and/or snow walls. However, the balances could never be completely sheltered from wind due to the need to see the birds' colour-rings. The degree to which wind affected the balances was monitored regularly throughout observation periods by noting the maximum deviation on the zeroed balance within 10s. In total, 31% of the 3763 readings were obtained when the maximum deviation in 10s was 0.5g, 25% with maximum deviations of 0.6-1.0g, 36% with maximum deviations of 1.1-2.0g, and 8% when the maximum deviation was more than 2.0g. These categories were scored 4, 3, 2 and 1 respectively, and used as weighting factors when working out mean daily masses, etc. (thus giving greater emphasis to readings obtained when winds were light). The daily mass pattern of each individual was inspected by eye, and a small proportion of readings (1.6%) which obviously differed from the rest, and were almost certainly the result of recording error (false identification, read-out read incorrectly, etc.), were omitted.

Altogether 2975 mass readings were obtained from 89 individually marked birds on 38 different days. These 38 days were divided amongst 12 bouts of 1-11 days duration, when balance readings were obtained on a near-daily basis. Up to 261 readings were obtained in a day (median=70 readings), from up to 39 individuals (median=18 individuals). Five or more birds were weighed on 84% of days when readings were obtained, 10+ on 68% of days. The number of observations per bird in a day varied between one and twenty-six (median=3). The median number of days on which individuals were weighed was four, but 44 birds were weighed on at least five days, 27 on at least ten days, and one male on 27 different days. There was therefore considerable scope for individual patterns of mass change to emerge.

8.2.3 Definitions of experience and dominance

In analyses using only the trapped sample of birds, prior site experience was again defined, as in **7.3.3a**, in three categories of increasing site experience: unringed birds when first caught, birds first caught earlier in

the same winter, or birds first caught in a previous winter. When looking for effects of experience on mass or fat variables, I omitted re-trappings of birds within ten days of a previous trapping to ensure independence of data and remove any handling effects. When analysing the data from the electronic balances, however, I was unable to use the data from unringed birds because I could not ascribe them to particular individuals. Experience was hence limited to two categories of ringed birds, depending on whether they were first caught earlier in the same winter, or in some previous winter.

Dominance was estimated by an individual's win proportion when adult (WPA, see **7.3.3d**). Similar results were obtained if birds were credited with higher dominance status when juvenile (see **7.3.3**), and so are not reported here. As measurements of aggression were not begun until 1988/89, and many birds left Cairn Gorm before an estimate of their WPA could be obtained, samples used to test for variation associated with dominance were lower in some analyses.

8.3 RESULTS

8.3.1 Effect of wing-length and sex on body-mass

Body-mass increased markedly, and almost linearly, with fat score in both sexes (**Fig.8.1**; oneway ANOVAs: females $F_{5,2117}=389.2$, $P<0.001$, males $F_{5,1153}=295.1$, $P<0.001$).

The majority of birds handled had a fat score of 1 (64% of 2123 females, 60% of 1159 males). I therefore examined the influence of wing-length and sex on body-mass within this fat category. Body-mass was positively correlated with wing-length, and the slope of the regression did not differ between genders (**Fig.8.2**; MANOVA with sex x wing-length interaction term, effect of interaction: $F_{1,1862}=0.30$, $P=0.58$). However, for a given wing-length, males were significantly heavier than females (MANOVA without interaction term, effect of sex: $F_{1,1863}=152.9$, $P<0.001$). Within males, the slopes of the regressions did not differ between fat categories (MANOVA with fat x wing-length interaction term, effect of interaction: $F_{5,1059}=1.48$, $P=0.19$). A similar result was obtained for females if the small sample (2%) of birds with fat scores of 4 and 5 were omitted (MANOVA, effect of fat x wing-length interaction term: $F_{3,1869}=0.35$, $P=0.79$). In conclusion, for a given amount of energy reserves (as estimated by fat score), body-mass was positively correlated with body-size (as estimated by wing-length). The relationship was consistent across a wide range of fat levels, but also had a strong sex-specific component.

8.3.2 Mass loss during handling

It is well known that birds lose mass between capture and weighing, and that the rate of mass loss is highest soon after capture (for review see Zwarts *et al.* 1990). Some studies attempt to control for this mass loss by adding an amount to the measured mass in relation to how long the individual has been held (e.g. Zwarts *et*

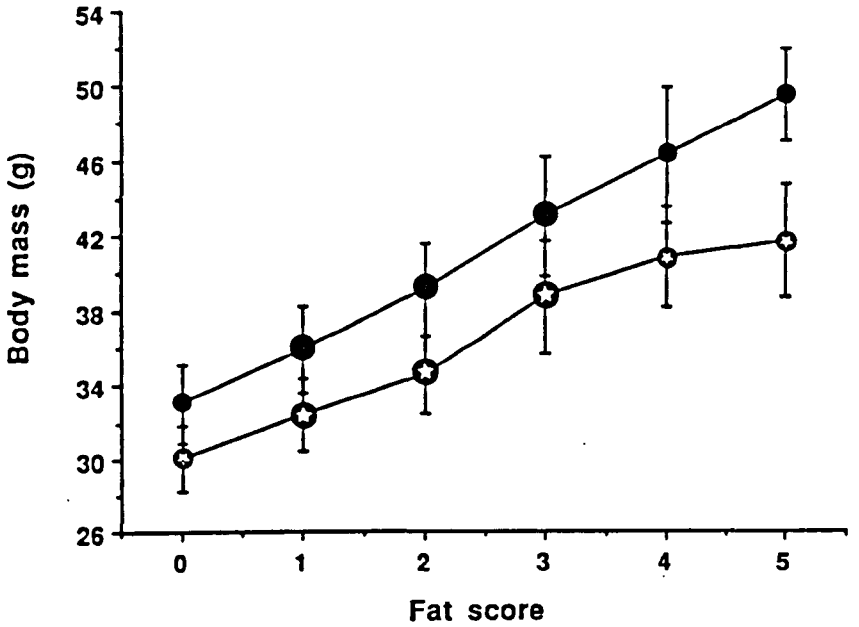


Fig.8.1. Body-mass (± s.d.) increases with fat score in both male (filled circles) and female Snow Buntings (starred circles). *Small symbols represent samples of 10-50 weighings, large symbols samples of 75-1400 weighings.*

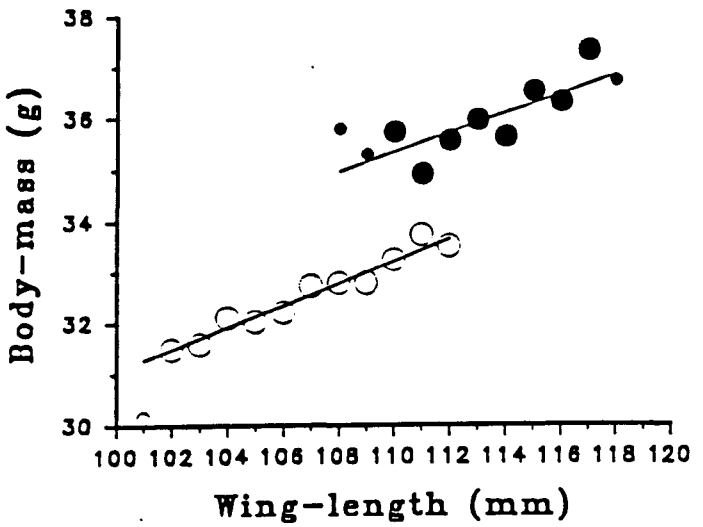


Fig.8.2. The relationship between body-mass and wing-length in female (open circles) and male (filled circles) Snow Buntings with a fat score of 1. *Small symbols are means of 5-20 birds, large symbols are means of larger samples. Within-sex regression lines are shown, but the slopes of these were statistically indistinguishable (see text). The combined slope (B=0.205) was highly significant (MANOVA, effect of wing-length covariate, t=9.79, P<0.001).*

al. 1990). Others, generally those where birds were weighed soon after capture, treat variation in mass loss as 'noise' and do not correct for it (e.g. Gudmundsson *et al.* 1991). This section therefore describes rates of mass loss in two winter Snow Buntings catches, where individuals were weighed twice during the period they were held captive, and discusses the pros and cons of attempting to correct my Snow Bunting masses for variation in handling time.

Individual rates of mass loss in the two catches varied between 0.0g/hour and 2.1g/hour (**Fig.8.3**). I conducted a stepwise multiple regression analysis on the rate of mass loss, including day, body-mass when first measured, the length of time elapsed between capture time and the first weighing (square-root transformed to normalise the data), and the length of time between weighings as independent variables. Only the length of time until the first weighing explained a significant proportion of the rate of mass loss (**Fig.8.4**; r_{40}=0.70, P<0.001): mass losses were highest if birds were first weighed soon after the catch, but gradually declined with time from capture. The rate of mass loss did not appear to continue to decline in birds first weighed more than 30 minutes after capture (r_{16}=-0.03, P=0.90), averaging 0.43g/hour thereafter. However, this was still almost double the overall rate of mass loss shown by a bird stunned during trapping and held, in the hope that it would recover, for two days until its eventual death (**Fig.8.5**).

The higher rates of mass loss within the first 30 minutes of capture probably mainly represent processing of food in the gut and defecation (Zwarts *et al.* 1990). Energy use may also be greater at this time because birds may struggle more, and anxiety levels may be higher. Few birds (mostly those in very small catches) were weighed within 30 minutes of capture, because of the time taken to release the birds from the net, reset the net, and prepare the ringing equipment. Although small catches (1-4 birds) were the most frequent, birds in small catches formed only a small part of the total sample (**Fig.8.6**). Most birds were released within 90 minutes (fewer measurements were taken from birds in larger catches to achieve this turnover), especially in the Early/Mid Winter sample from Cairn Gorm where catches of 10-20 were relatively more frequent (**Fig.8.6**). Therefore, on average, the last birds to be released may have lost up to 0.5g more than the first birds to be released.

I chose not to correct for mass loss during weighing because (i) the time of weighing relative to the catch time was not usually recorded, (ii) it was not always possible to retrospectively ascertain the order in which birds were weighed, (iii) birds of a particular age, sex or experience category were not weighed in any given order, and (iv) body-mass after 30 minutes in captivity may give a better indication of a bird's *energy* reserves than its mass at capture. A delay of thirty or more minutes may help reduce variability due to the amount of food or faeces in the gut, dampness of plumage, etc. Although individuals in larger catches were dealt with more quickly, it is still inevitable that the average time between capture and weighing was greater in such birds. In the next section (**8.3.3**), I therefore included a test for a relationship between MASS RESIDUAL and the size of the catch (log10-transformed), to find out whether the size of these differences is likely to have affected the results.

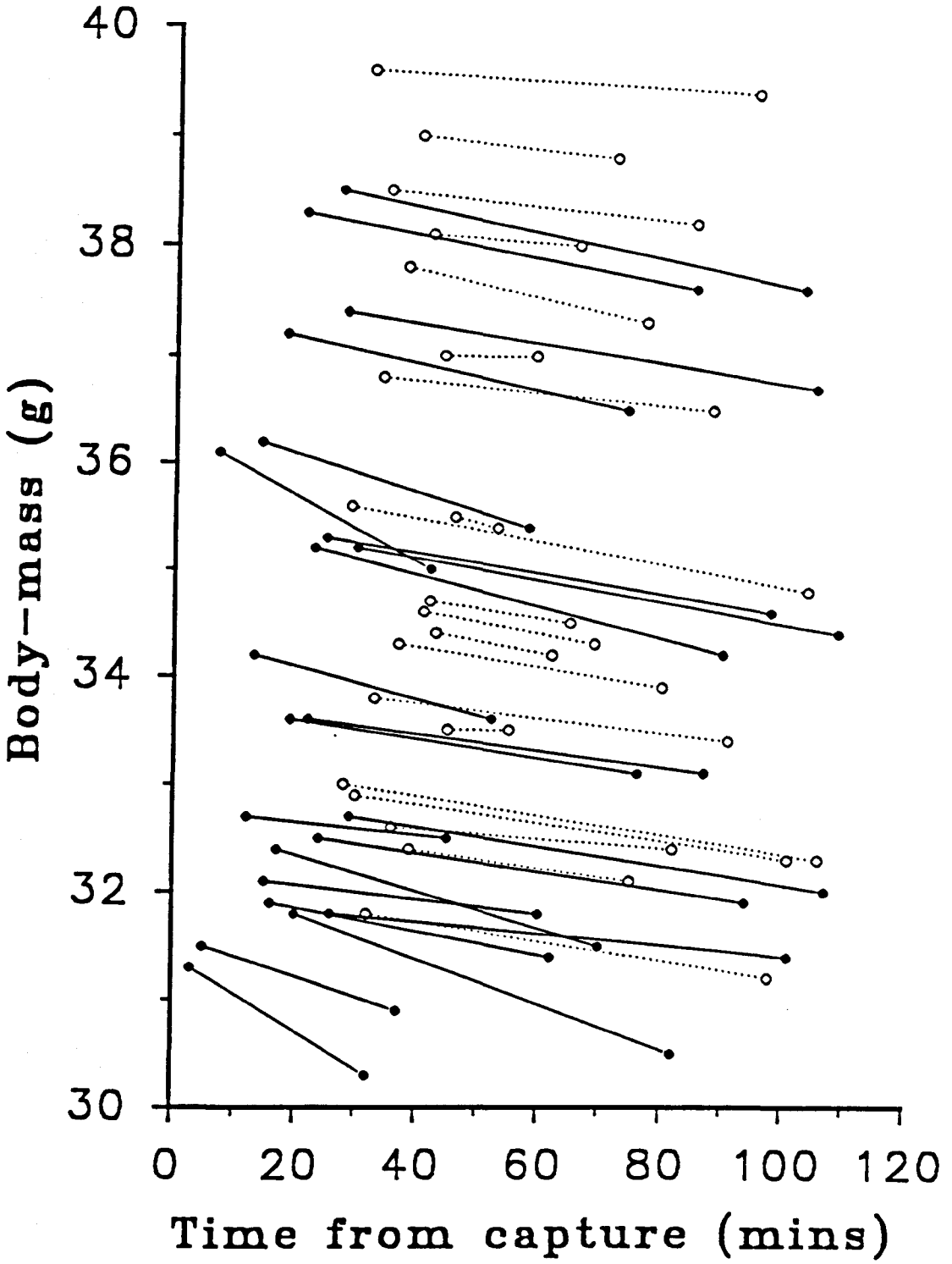


Fig.8.3. Mass loss in two catches of Snow Buntings where individuals were weighed twice during the period they were held captive. *Lines connect consecutive masses of the same bird. Solid symbols and lines represent birds caught on 31st January 1993 (n=22), open symbols and broken lines those caught on 21st February 1994 (n=20).*

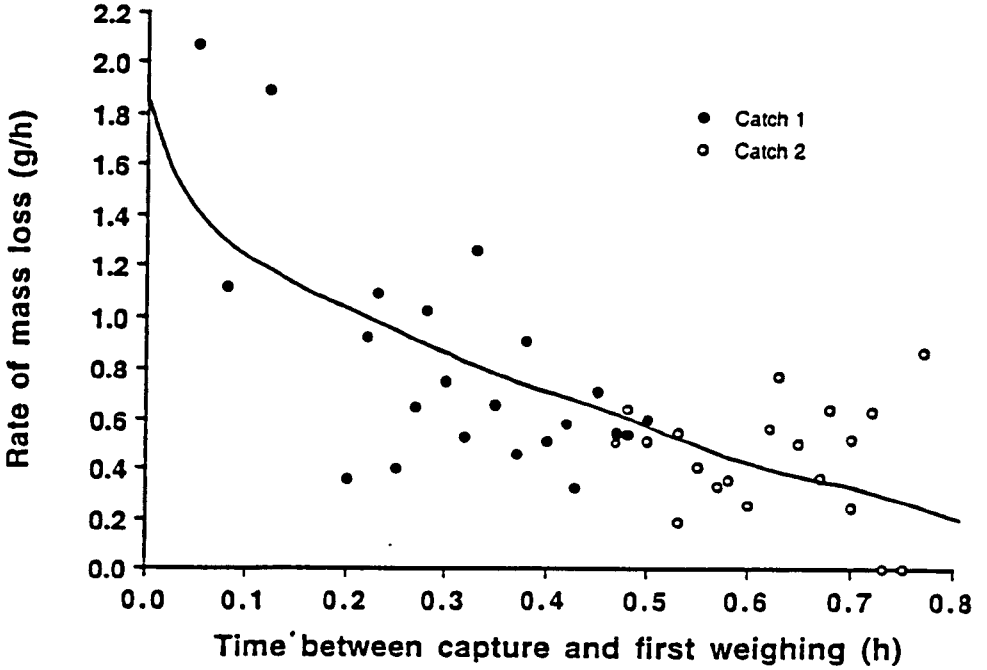


Fig.8.4. Rate of mass loss between weighings of Snow Buntings weighed twice during the period they were held captive, in relation to the time taken before making the first of these weighings. *Solid and open symbols represent different catches, as in Fig.8.3. The fitted line is the slope of the regression between rate of mass loss and the square-root transformed time between capture and first weighing (see text). Rate of mass loss decreased with time after capture, levelling off after about 30 minutes (see text).*

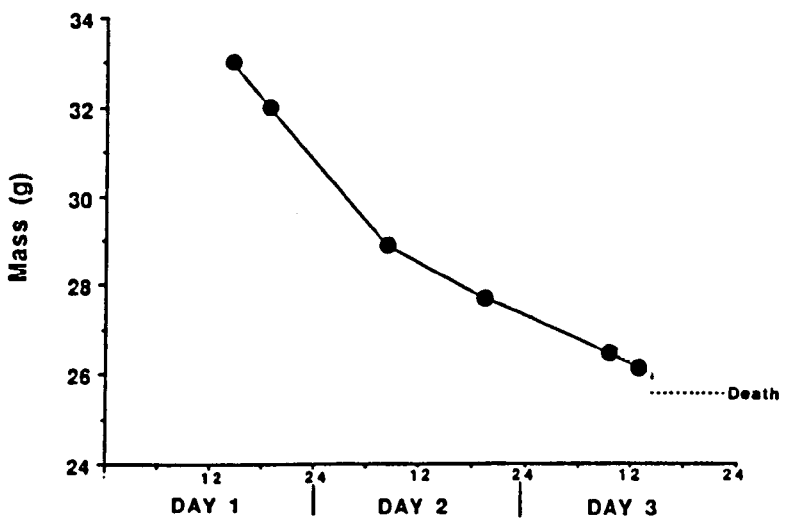


Fig.8.5. Mass loss of a stunned female Snow Bunting held over a three-day period until its eventual death (at 25.6g, presumably from starvation). *Points represent consecutive weighings. In total the bird lost 7.2g in approximately 48 hours, a mean mass loss of 0.15g/hour.*

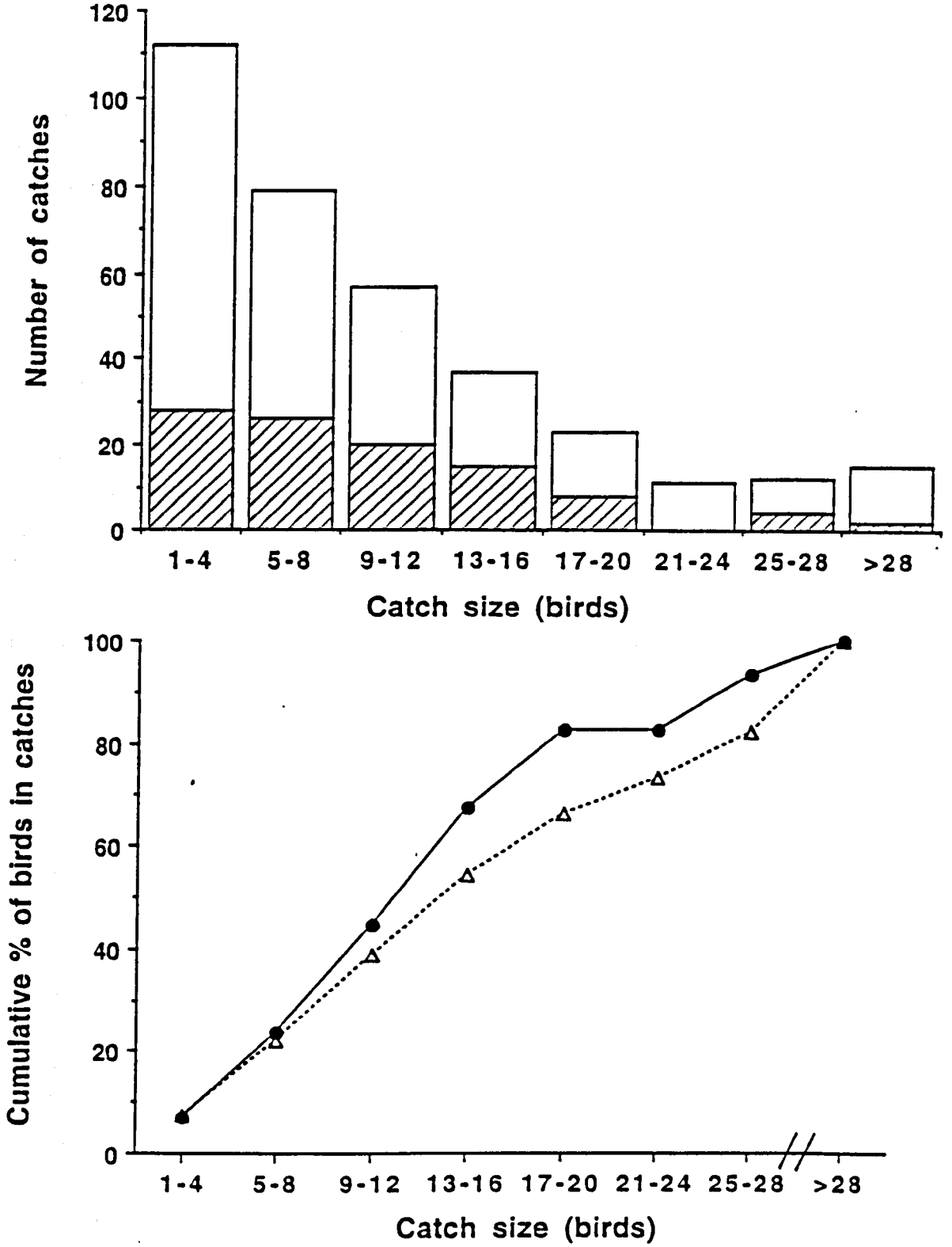


Fig.8.6. The number of catches (a), and the cumulative percentage of birds caught in catches (b), of a particular size. *Birds in catches at all sites at all times (n=3483) are represented by open bars (a) and open symbols (b); those on Cairn Gorm in Early/Mid Winter (n=971) are shown by hatched bars and filled symbols.*

8.3.3 Diurnal, seasonal and weather-related influences on body-mass

At the three upland ski areas, sex and wing-length accounted for about half of the observed variation in Early/Mid Winter body-mass (**Table 8.1**). Over the day, mass increased at 3.9g/hour on Cairn Gorm and 2.5g/hour at Glen Shee. On Cairn Gorm, where catches were made most regularly and the total sample was more than double that at the other sites, the regression slopes for DAY & DAY^2 were also both significant, but they were opposite in sign. This results in a seasonal pattern of increase then decline in mass, peaking in mid-January (curves on **Fig.8.7**). This relationship was still obvious if mean body-mass on each catching day was used (see points on **Fig.8.7**). The MASS RESIDUALs from the Cairn Gorm sample were unrelated to catch size (correlation of MASS RESIDUAL and log10 catch size: r_{961}=-0.03, P=0.36).

Bait was almost always available to Snow Buntings on Cairn Gorm because I attempted to make visits there on almost every day that snow fell. Visits to other sites were less frequent, and were given lower priority than visits to Cairn Gorm. Hence supplemental food at my feeding stations at Glen Shee and The Lecht may have been totally eaten or unavailable (due to the accumulation of snow) for several days prior to a catching visit. This may have prevented birds from following any seasonal pattern of fat storage at these sites, or obscured the detection of seasonal trends if birds were often caught on occasions when they were using their energy reserves. As weather was only recorded on Cairn Gorm (the three upland sites often varied dramatically in the occurrence and extent of snowfalls, despite their proximity to each other), and there was evidence at that site that birds followed a mid-winter fattening strategy, I looked for effects of weather conditions on MASS RESIDUALs at Cairn Gorm alone.

Table 8.2 shows the relationships between MASS RESIDUAL and a selection of weather variables. Using the whole sample of Early/Mid Winter masses from Cairn Gorm, the data appear to be consistent with the hypothesis that birds lose mass in bad conditions, except for the positive correlations between MASS RESIDUAL and the wind variables. However, as discussed in **8.2.1**, these data are probably best analysed at the level of the catch rather than the individual. I therefore calculated the mean of the MASS RESIDUALs for each catch (MEAN MASS RESIDUAL), and again compared this to weather variables (**Table 8.2**). Only catches of five or more birds were selected because this would reduce variation caused by deviations of the sample mean from the actual mean in small catches. Three weather variables were still associated with variation in body-mass (**Table 8.2**): MEAN MASS RESIDUAL decreased as the number of consecutive days with at least partial snow cover increased (**Fig.8.8**), when there was at least partial snow-cover on the catch day (**Fig.8.9a**), or when there had been at least partial snow cover present on either the catch day or the day before (**Fig.8.9b**). The relationship between MEAN MASS RESIDUAL and this latter variable was the strongest, explaining 18% of the observed variation.

Table 8.1. Multiple regression of body-mass (g) on independent variables in Early/Mid Winter Snow Buntings at three upland catching sites. *Significant variables are listed in the order that they were included by the stepwise procedure. TIME of day measured to the nearest 15 minutes, DAY is days from 1st October.*

Site	n	Independent Variable	B	Partial correlation coefficient	P	Cumulative r^2
Cairn Gorm	963	SEX	2.78	0.30	***	0.38
		TIME	0.39	0.38	***	0.46
		DAY	0.15	0.24	***	0.48
		DAY^2	-0.000664	-0.23	***	0.50
		WING-LENGTH	0.20	0.18	***	0.52
		Constant	-3.49			
Glen Shee	453	SEX	2.33	0.28	***	0.40
		TIME	0.25	0.26	***	0.44
		WING-LENGTH	0.24	0.25	***	0.48
		Constant	1.84			
		DAY		0.03	0.58	
		DAY^2		0.03	0.49	
The Lecht	375	SEX	3.14	0.30	***	0.38
		WING-LENGTH	0.14	0.18	***	0.52
		Constant	14.92			
		TIME		0.04	0.43	
		DAY		-0.01	0.95	
		DAY^2		0.04	0.91	

*** P<0.001, ** P<0.01, * P<0.05

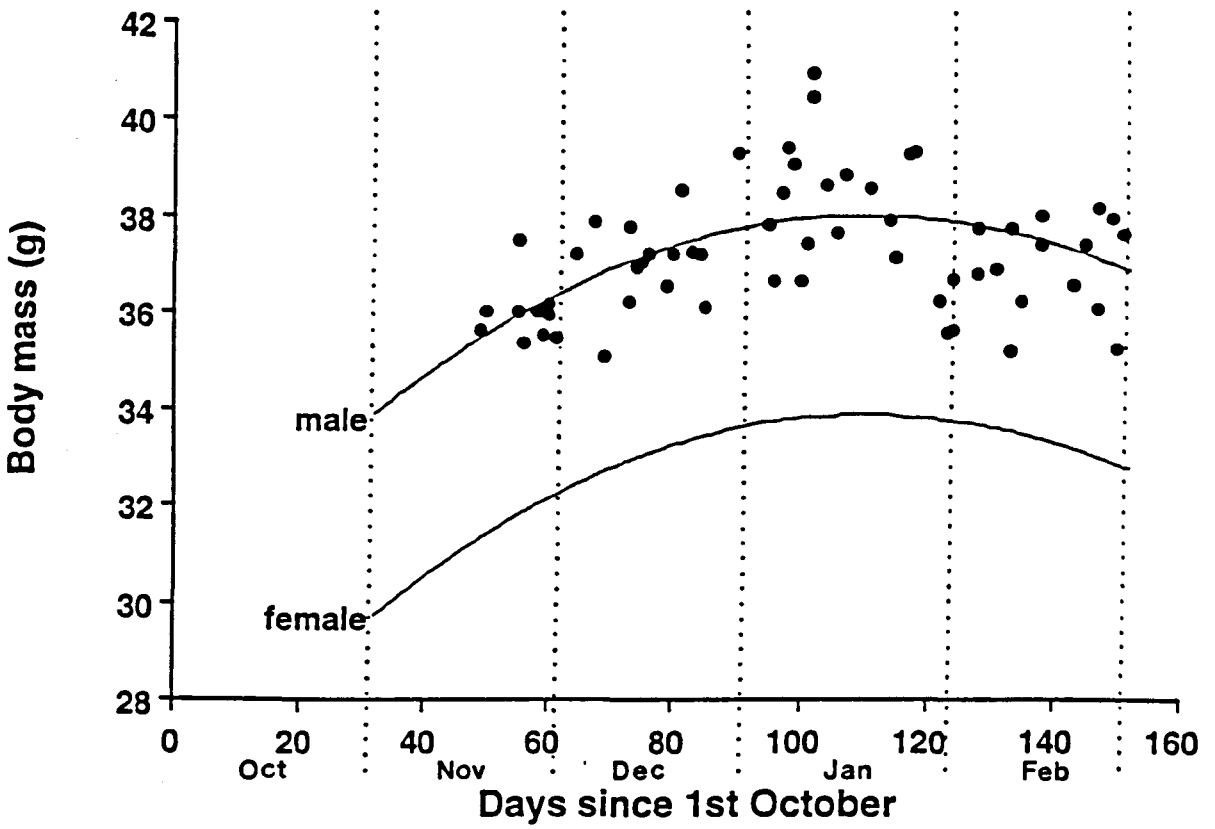


Fig.8.7. Seasonal changes in mean noon mass of male and female Snow Buntings of average size on Cairn Gorm (curves based on 963 weighings of individual birds, see Table 8.1 for analysis). *Points represent the mean body-mass of Snow Buntings caught on each of 62 days when five or more birds were caught, standardised to the equivalent masses of average-sized males at noon (see Table 8.1). A multiple regression analysis of mean body mass from these 62 catches, entering the independent variables DAY and DAY² together, found that both variables were still significant predictors of mean catch body-mass (DAY: regression slope B=0.17, t associated with slope=4.74, P<0.001; DAY², B=-0.00078, t=4.51, P<0.001).*

Table 8.2. The relationship between MASS RESIDUAL (of individuals) or MEAN MASS RESIDUAL (of catches) and weather variables (see 2.3 for more detailed description of variables). *Pearson correlations are given for weather variables with normal distributions, Spearman Rank correlations for continuously distributed variables which showed a strong deviation from normality (denoted with $). Oneway ANOVAs were used to look for significant effects of more categorical variables on MASS RESIDUAL and MEAN MASS RESIDUALS. Sample sizes are 963 individual MASS RESIDUALs and 62 MEAN MASS RESIDUALS (based on catches of 5+ individuals), except for 9AM TEMPERATURE and variables derived from it which were unavailable in 1987/88, reducing samples to 608 and 41 respectively.*

	MASS RESIDUAL		MEAN MASS RESIDUAL	
Variable	r	P	r	P
SNOW COVER (3-DAY MEAN) $	-0.09	**	-0.15	0.24
SNOW COVER (6-DAY MEAN) $	-0.13	***	-0.19	0.13
CONSECUTIVE DAYS SNOW COVER $	-0.17	***	-0.31	*
9AM TEMPERATURE	0.11	**	0.22	0.16
9AM TEMPERATURE PREVIOUS DAY	0.07	0.09	0.16	0.33
9AM TEMPERATURE (2-DAY MEAN)	0.10	*	0.22	0.17
MEAN TEMPERATURE	0.03	0.43	0.09	0.49
MEAN TEMPERATURE PREVIOUS DAY	0.05	0.10	0.17	0.18
MEAN TEMPERATURE (2-DAY MEAN)	0.04	0.18	0.14	0.26
WIND SPEED	0.04	0.25	0.10	0.42
WIND SPEED PREVIOUS DAY	0.08	*	0.17	0.19
WIND SPEED (2-DAY MEAN)	0.07	*	0.16	0.21

	MASS RESIDUAL			MEAN MASS RESIDUAL		
Variable	d.f.	F	P	d.f.	F	P
SNOW DEPTH a	2,960	0.07	0.93	2,59	0.27	0.76
SNOW DEPTH PREVIOUS DAY a	2,960	0.18	0.83	2,59	0.07	0.93
SNOW COVER	2,960	10.34	***	2,59	3.90	*
SNOW COVER PREVIOUS DAY	2,960	6.02	**	2,59	1.33	0.27
SNOW COVER (2-DAY MEAN) b	2,960	16.97	***	2,59	6.41	**

*** P<0.001, ** P<0.01, * P<0.05

a 3 categories: no snow, 0-9cm of snow & 10+cm of snow.

b Few birds or catches with 2-day mean SNOW COVER scores of 0.5 or 1.5, so these were grouped with scores of 1 & 2 respectively to give 3 categories (0, 1 & 2).

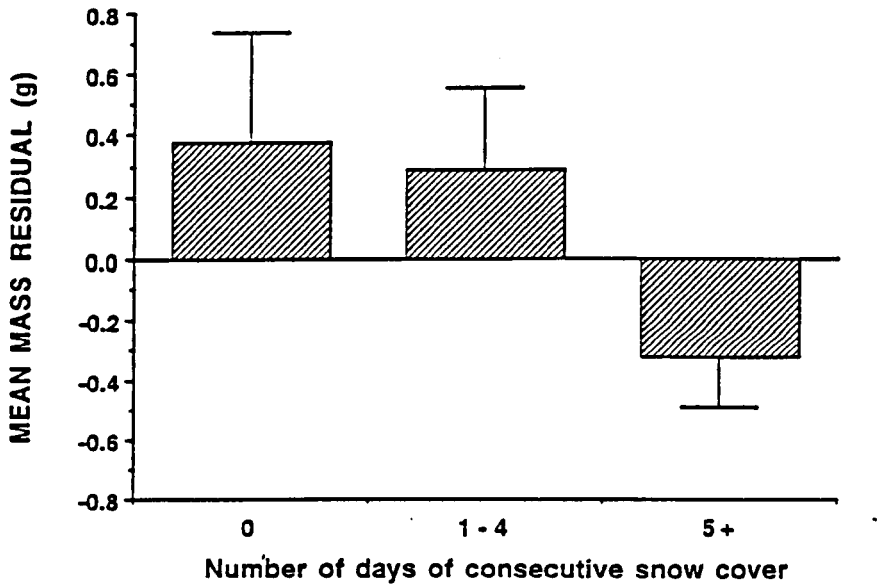


Fig.8.8. MEAN MASS RESIDUAL (± s.e. bar) of Early/Mid Winter Snow Bunting catches on Cairn Gorm against the number of successive days with at least partial snow cover prior to the catch. *Only catches with five or more birds trapped were included. Sample sizes (left to right) are 14, 12 & 36 catches.*

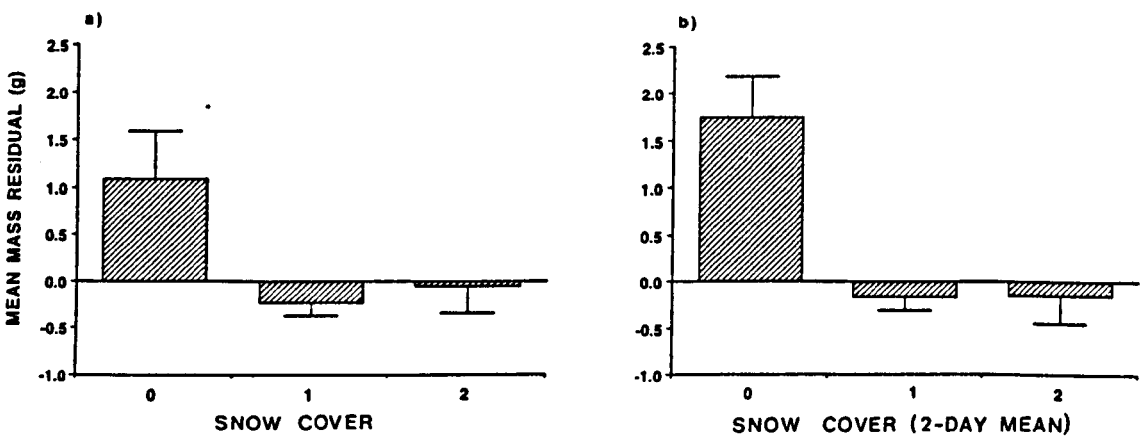


Fig.8.9. The relationship between the MEAN MASS RESIDUAL (± s.e. bar) of Early/Mid Winter catches of Snow Buntings and (a) catch-day SNOW COVER (0=no snow or ice, 1=partial snow cover, 2=complete snow cover, see 2.3), and (b) the mean of SNOW COVER on the catch day and the day previously. *Only catches of 5+ birds were considered. Sample sizes (left to right) are 6, 34, 22, 4, 38 & 20 catches. Birds were heavier than expected on days with no snow or ice cover, especially if these conditions had persisted from the previous day (see Table 8.2 for statistics).*

Two factors prevented me from gauging the relative contribution of each weather variable to body-mass variation. Firstly, there were only six catches of more than five birds on snow-free days. Secondly, the weather variables which were significantly related to body-mass variation were not independent. This was because they were partly derived from the same original measurements (e.g. SNOW COVER, 2-day mean SNOW COVER and CONSECUTIVE DAYS SNOW COVER), and because snowy, rather than snow-free ground conditions were more likely to follow a run of several days of partial snow-cover. MEAN MASS RESIDUALS appeared to be lower if either the present day or the previous day had at least partial snow-cover, but there was little evidence of an additive effect (**Fig.8.10**). A similar result was obtained with SNOW COVER and CONSECUTIVE DAYS SNOW COVER.

8.3.4. Individual influences on body-mass

The effects of sex and size (wing-length) on MASS RESIDUAL were controlled for in the original multiple regression analysis. Therefore, I looked for effects of age, experience and dominance within each sex category. I also examined whether three weather variables (SNOW COVER, SNOW COVER PREVIOUS DAY and CONSECUTIVE DAYS SNOW COVER) had any influence on how age, experience or dominance were related to MASS RESIDUAL. They were introduced as additional variables in separate ANOVAs (all with two categories: SNOW COVER & SNOW COVER PREVIOUS DAY with snow-free versus at least partial snow-cover, CONSECUTIVE DAYS SNOW COVER with 3 or less successive days of snow-cover versus 4+ successive days snow-cover). The 2-day mean SNOW COVER, although possibly the most influential weather variable (**Fig.8.9b**), could not be used because only 6% of 893 available MASS RESIDUALs were obtained when both the catch day and the previous day were snow-free.

Adult females had higher MASS RESIDUALs than juvenile females, but there was no significant difference beteen adult and juvenile males (**Fig.8.11**). There were no significant interactions between the weather variables and age in either sex (minimum P for weather x age interaction in six 2-way ANOVAs=0.09). Within age/sex categories, there was no effect of experience on MASS RESIDUAL (oneway ANOVA: $P>0.13$ in all four age/sex categories). Again weather appeared to have little impact on this result because only one of the twelve 2-way ANOVA age/sex x weather interactions showed even marginal significance (SNOW COVER x experience in juvenile females: same-year retraps heavier than new birds in snow-free conditions, but lighter when some snow-cover, $F_{1,139}=4.06$, $P=0.046$).

Within gender, I also examined the relationship between dominance (win proportion when adult, WPA) and MASS RESIDUAL. There was no significant correlation between WPA and MASS RESIDUAL in either sex (females $r_{57}=-0.07$, $P=0.62$; males $r_{170}=-0.11$, $P=0.16$). I again looked for a modifying role of weather conditions on this result by comparing the regression lines in different weather conditions using MANOVA. Only males were tested because the sample was larger, they showed a wider range of WPAs, and, unlike in females (above), age was not known to influence body-mass. Once more, however, the

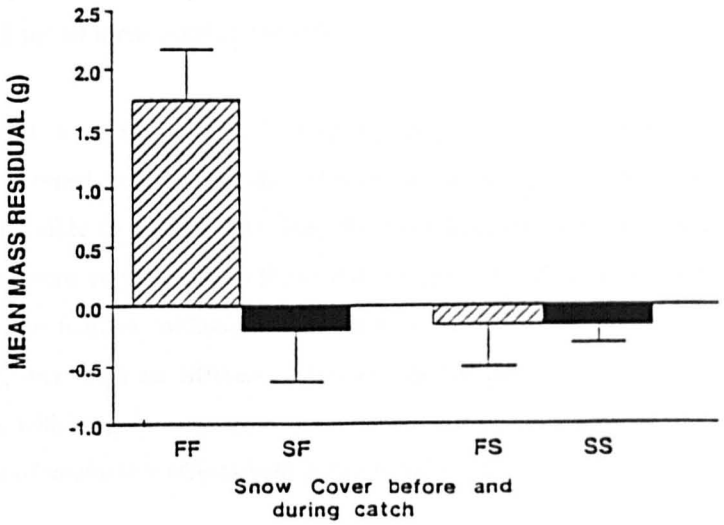


Fig.8.10. The combined effect of the catch-day's SNOW COVER and the previous day's SNOW COVER on the MEAN MASS RESIDUAL (± s.e. bar) of a catch. *Combinations of F and S (representing snow-free and snowy conditions respectively) show the weather on the day before and the day of the catch respectively (e.g. SF = snow lying on the previous day, but not the catch day). Sample sizes (left to right) are 4, 2, 10 & 46 catches. Whether or not the present day's ground conditions influenced body-mass variation depended on the previous day's ground conditions: they were not additive (ANOVA on MEAN MASS RESIDUAL with SNOW COVER and SNOW COVER PREVIOUS DAY, aggregating partial and complete snow-cover categories in both weather variables, significance of interaction term:* $F_{1,58}=4.06$, $P=0.05$).

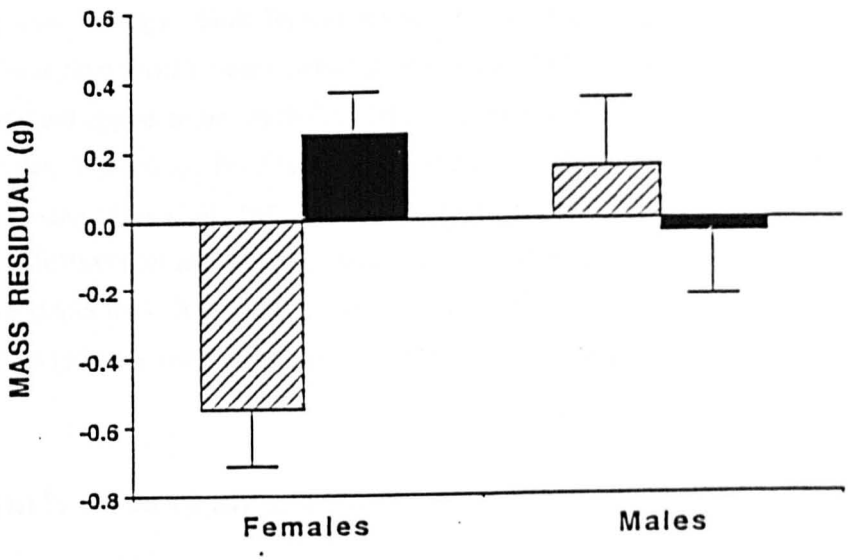


Fig.8.11. MASS RESIDUAL (± s.e. bar) in relation to a Snow Bunting's age and sex. *Hatched bars represent juveniles, and filled bars represent adults. Sample sizes (left to right) are 143, 312, 175 & 229 birds. Adults were heavier than juveniles in females* ($t_{453}=3.83$, $P<0.001$), *but not males* ($t_{402}=0.72$, $P=0.47$).

result was unchanged in different weather conditions (significance of weather variable x WPA covariate interaction, P>0.28 for all three weather variables).

MASS DEVIATION, a measure of an individual's body-mass *in relation to the body-masses of its catch-mates*, was assumed to be independent of seasonal, diurnal or weather-related variation (see **8.2.1**). Thus it was also possible to include data from the other trapping sites when analysing this variable. In general, the results were very similar to those given above for MASS RESIDUALs: adult females were heavier than juvenile females (although the difference in means was only 0.42g, versus 0.79g in the previous analysis), there was no difference between age categories in males, no difference between the experience groups within age/sex categories, no evidence that dominance affected MASS DEVIATION, and little evidence of interactive effects with weather conditions.

The direct use of visible fat deposits (as measured by fat score) for measuring energy reserves, has the advantage over body-mass of reducing variation due to gut contents, water balance, etc. (Blem 1990). Further, it does not require adjustments for sex, age or body-size. Its major drawbacks are its limited ordinal scale and the subjective classification of the fat score intervals. Although **Fig.8.1** indicates that fat score is almost directly proportional to body-mass, only 0.1% of Early/Mid Winter fat scores were more than 3, and some 96% were either 1 or 2. Hence, even though FAT DEVIATION is a measure of an individual's fat score in relation to the mean fat score of the catch, and therefore approached a normal distribution, the results should still be treated with caution.

Most interestingly, there was variation in FAT DEVIATION amongst the age/sex categories, mainly because males had relatively larger fat scores than females (**Fig.8.12**). This was not simply because fat score was greater in larger birds because no significant relationship between FAT DEVIATION and wing-length was found *within* sexes (females: r_{924}=-0.03, P=0.42; males: r_{540}=0.08, P=0.07). Prior site experience did not appear to influence FAT DEVIATION within age/sex categories (oneway ANOVAs: juvenile females, $F_{1,368}$=0.31, P=0.58; juvenile males, $F_{1,286}$=0.70, P=0.40; adult females, $F_{2,555}$=0.08, P=0.92; adult males, $F_{2,252}$=2.66, P=0.07). Nor was FAT DEVIATION related to dominance (correlations between FAT DEVIATION and WPA in males: r_{101}=-0.00, P=0.98; females: r_{41}=-0.04, P=0.82). As in the analyses with MASS RESIDUAL and MASS DEVIATION there was no consistent evidence that patterns of FAT DEVIATION in relation to age, sex, experience or dominance were influenced by weather conditions.

8.3.5 Hourly rates of mass gain

Earlier, from single measurements from many different Snow Buntings, I estimated average rates of body-mass increase as birds foraged on winter days (**Table 8.1**). This section investigates the rates of mass gain of *individuals* which were attracted to the electronic balances, and looks for trends within the winter,

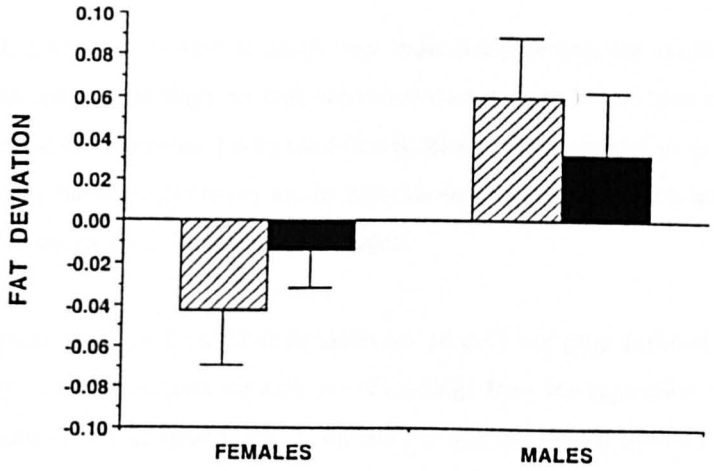


Fig.8.12. FAT DEVIATION (± s.e. bar) in relation to a Snow Bunting's age and sex. *Hatched bars represent juveniles, stippled bars are adult birds. Sample sizes (left to right) are 370, 558, 288 & 255 birds. Males were fatter than females, but there was little difference between age groups (2-way ANOVA: effect of sex $F_{1,1467}=8.53$, $P=0.004$; age, $F=0.08$, $P=0.78$; interaction, $F=1.32$, $P=0.25$).*

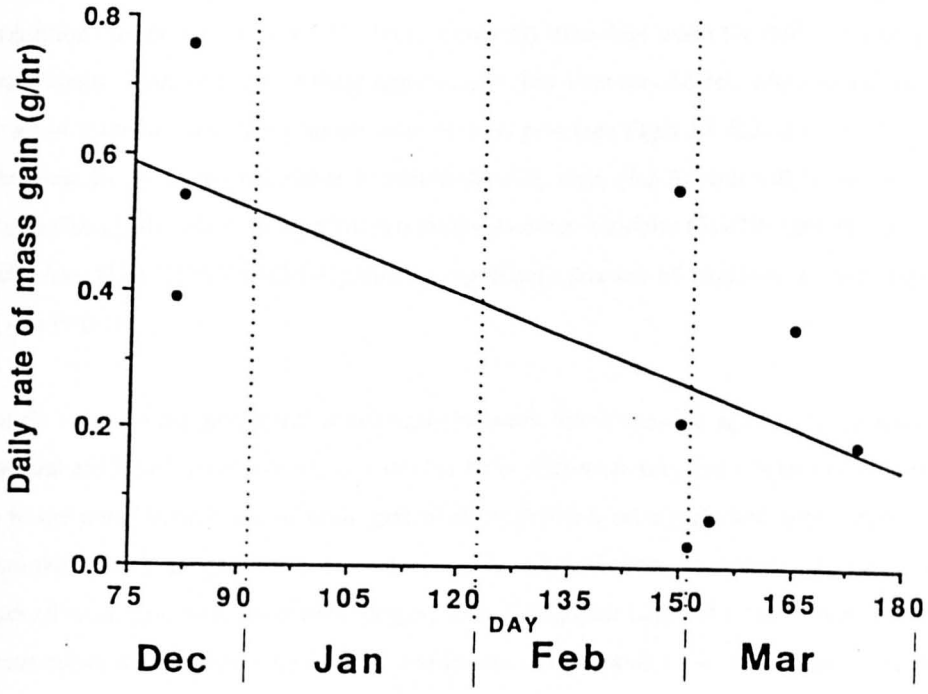


Fig.8.13. The mean hourly rate of mass gain of Snow Buntings in relation to winter date (DAY: days from 1st October). *I have only included days when the hourly rate of mass gain of at least three individuals was measured. The mean hourly rate of mass gain was lower in spring than winter: mean rate= -0.004DAY+0.90, $r_7=-0.67$, $P=0.049$ (also see text).*

variation associated with weather conditions, and differences between individuals.

Hourly rates of mass gain (g/hour) were obtained from individuals visiting the electronic balances if, on a given day, there were balance readings for that individual over at least a four hour spell. Additionally, to improve the accuracy of the estimates, I only used hourly rates of mass gain based on at least five readings for the individual when the wind deviation on the balance was 1g or less, or at least ten readings for the individual if wind deviations up to 2g had to be included.

In total, 68 sets of mass readings from 38 individuals on 16 different days fulfilled these criteria. I then calculated the hourly rate of mass gain for each set of readings from the regression of mass on time. The mean rate of mass gain was 0.32g/hour (s.d.= 0.26g/hour, n=68) and ranged from a loss of 0.23g/hour to a gain of 0.87g/hour.

The mean rate of mass gain varied between 0.03g/hour and 0.76g/hour on nine days when it could be measured in three or more individuals. There was significant variation in hourly rates of mass gain between these nine days (oneway ANOVA: $F_{8,50}=9.12$, $P<0.001$). The mean hourly rate of mass gain was higher in winter than spring (**Fig.8.13**; grouping days in December versus late February/March $t_7=2.45$, $P=0.044$).

I was unable to make a compelling comparison between the mean hourly rates of mass gain in different weather conditions for two reasons. Firstly, there were only nine days when the rate was measured in three or more individuals. Moreover, six of these days were in late February/March when longer daylight hours alone may allow birds to reduce their hourly rates of mass gain (see **Fig.8.13, 8.3.6**). Secondly, snow-cover, perhaps the most likely weather variable to reduce feeding rates (**8.3.3**), was 100% on all nine of these days. Not surprisingly therefore, none of the remaining weather variables (SNOW DEPTH, WIND SPEED, MEAN and 9AM TEMPERATURES) explained a significant amount of variation in mean hourly rates of mass gain (all $P>0.18$).

Did the hourly rate of mass gain differ consistently between Snow Bunting age or sex categories, or some other individual attribute? To answer this, I calculated the relative hourly rate of mass gain of an individual in relation to the mean hourly rate of mass gain of all individuals on a particular day. Again, I could only use the nine days when at least three individual hourly rates of mass gain were measured. In total, 59 relative rates of mass gain were measured, ranging from 0.35g/hour below the daily mean rate of mass gain to 0.63g/hour above the average. The relative hourly rate of mass gain of six individuals was measured on three or more days. There was no indication that the relative rates of mass gain of these individuals differed consistently from each other (oneway ANOVA: $F_{5,15}=1.27$, $P=0.33$). Similarly, treating all 59 measurements of relative rate of mass gain independently, there was no evidence that age, sex, previous site experience, breeding status, dominance status or size influenced an individual's relative rate of mass gain (oneway ANOVAs or regressions, all $P>0.36$). Once more, however, low sample sizes considerably

reduced the power of these tests.

8.3.6 Rates of overnight mass loss

A constant hourly rate of mass gain, as calculated in the multiple regressions given in **8.3.3**, is not realistic because the ratio of day- to night-length changes throughout the winter. If birds increased mass at 0.39g/hour both in mid-winter and in late February, the overnight rate of mass loss would have to be twice as high in late February if dawn mass was to remain constant between days. The previous section suggests an alternative scenario: Snow Buntings gained mass more quickly during mid-winter days than in late winter (**Fig.8.13**). Differences in the observed average hourly rates of mass gain measured during two different parts of the non-breeding season (**Fig.8.13**) would then be balanced by similar rates of overnight mass loss in each of these periods (0.20-0.22g/hour, **Table 8.3**). Slightly higher rates of overnight mass loss might be expected in mid-winter than late winter because temperatures are lower. Indeed, the difference between mid-winter and late winter overnight mass loss rates would be larger if birds began feeding relatively earlier in respect to dawn and ended later in respect to dusk in mid-winter compared to late winter.

Table 8.3. The calculation of overnight rates of mass loss from day-length, night-length and observed hourly rates of mass gain whilst feeding.

Date a	Rate of mass gain during day (g/hour) b	Day-length (hours) c	Night-length (hours) c	Rate of over-night mass loss (g/hour) d
21 December	0.56	6.68	17.32	0.22
6 March	0.24	11.02	12.98	0.20

a Mean dates from two groups of days on Fig.8.13.

b Taken from regression line on Fig.8.13.

c Difference between sunrise and sunset times in Aberdeen, as supplied by the 'Press & Journal'.

d (Rate of mass gain x Day-Length)/Night-Length.

8.3.7 Seasonal variation in dawn body-mass

Lehikoinen (1987) maintained that true winter fattening occurs only if the mean mass at *dawn* shows a seasonal peak in mid-winter. Thus **Fig.8.7**, showing a mid-winter peak in *noon* masses, is not sufficient evidence for true winter fattening because, in theory, the peak could be generated by a greater amplitude in daily mass gain in mid-winter even if dawn mass was constant or lower. Armed with an independent method for calculating hourly rates of mass gain (i.e. by rearranging the formula given in **Table 8.3**, and assuming a constant rate of overnight mass loss of 0.21g/hour, **8.3.6**), it was possible to reanalyse the Cairngorm Early/Mid Winter mass data to look for a mid-winter peak in *dawn* masses. The results were similar (**Table 8.4**): dawn mass peaked on 24/25th January at 36.4g for an average-sized male, compared to 34.6g on 1 December and 35.7g on 28th February. Snow Buntings on Cairn Gorm *do* therefore seem to follow a true mid-winter fattening policy.

Table 8.4. Multiple regression of dawn body-mass (g) on independent variables in Early/Mid Winter Snow Buntings on Cairngorm (n=962). *Significant variables are listed in the order that they were included by the stepwise procedure. Dawn body-mass was calculated from body-mass at the time of weighing by subtraction, assuming a seasonally varying rate of mass gain during the day (see text).*

Independent Variable	B	Partial correlation coefficient	P	Cumulative r^2
SEX	2.76	0.30	***	0.41
DAY	0.14	0.24	***	0.44
DAY^2	-0.000611	-0.21	***	0.47
WING-LENGTH	0.21	0.19	***	0.48
Constant	-0.77			

*** P<0.001, ** P<0.01, * P<0.05

8.3.8 Mass change between days

In **8.3.5** I examined the relationships between body-mass changes and both weather conditions and individual characteristics by looking at the hourly rate of mass gain of individuals *within* the daylight feeding hours. Assuming that these rates were effective estimates of the rate of mass gain throughout the whole day, and that overnight rates of mass loss were constant (a reasonable assumption between individuals, but perhaps not between weather conditions), then high measures of hourly rates of mass gain ought to result in mass increases between days, while low observed rates of mass gain should result in overall loss of body-mass between days. However, an alternative method of looking at how weather patterns or individual characteristics affect changes in body mass would be to look at changes in the body-mass of individuals *between* days.

I divided each day into 2-hour segments and selected balance readings from individuals which were available from the same two-hour segment on consecutive days. I then calculated the mean mass of that individual during each time segment on each day and measured the difference. To check whether this gave a consistent measurement, I examined the 80 cases where a bird was measured in more than one time period on a pair of days. If a bird was measured in more than two time segments on each of the pair of days I selected its earliest and latest pairs of measurements. As expected, these were positively correlated (r_{78}=0.53, P<0.001). I therefore took a mean daily value for each individual, weighted by a combination of the accuracy of balance readings (see **8.2.2**) and the number of readings in each two-hour spell (if one reading, weighting factor=1; 2-3 readings, wf=2, 4+ readings, wf=3). This then gave me a 24-hour mass change for each bird, i.e. its change in mass from one day to the same time on the next.

24-hour mass change varied between a loss of 5.4g and a gain of 4.1g. On average, birds gained 0.14g between days (s.d.=1.75g, n=220). To examine variation in 24-hour mass change between different days, I selected only days when the 24-hour mass change of at least five individuals was measured (n=13 days). The mean of individual 24-hour mass changes varied on a daily basis between a loss of 3.0g (n=5 individual 24-hour mass changes) and a gain of 1.4g (n=32), and showed significant variation between days (oneway ANOVA: $F_{12,189}$=13.2, P<0.001).

It is possible that daylength could have had an over-riding influence on the ability or willingness of birds to maintain or increase body-mass during snow spells (when all electronic balance data were obtained). Similarly the desire to fatten prior to migration could have increased the likelihood that birds would *gain* mass between days in Spring. However, there was no evidence that the mean 24-hour mass change varied between groups of observation days in January, late February/early March and mid-March (n=4,6 & 3 days respectively; oneway ANOVA, $F_{2,10}$=0.56, P=0.59). Nor could I find any association between mean daily 24-hour mass change and prevailing weather conditions (SNOW DEPTH, MEAN or 9AM TEMPERATURE, or WIND SPEED on either or both days, all P>0.20; SNOW COVER always 100%). It

is, of course, possible that daylength, weather and spring fattening influenced 24-hour mass changes simultaneously, but that the sample of days was too small to measure their independent effects. For example, 24-hour mass change was measured in five or more individuals on only four Early/Mid Winter days, preventing me from establishing whether weather conditions had a greater impact on mass changes when there were fewer available daylight hours.

24-hour mass change was measured on 202 occasions (n=55 individual Snow Buntings) on the 13 days when the 24-hour mass change of at least five individuals was measured (thus giving a sample average). On these days I calculated each individual's relative 24-hour mass change, i.e. its mass change minus the daily average. Overall, treating each measure of relative mass change independently (n=202), there was no relationship between either 24-hour mass change or relative mass change and age, sex, previous site experience, breeding status, dominance status or size (oneway ANOVAs or regressions, all $P>0.35$). Similarly, these attributes did not explain variation in the mean relative mass changes of 32 individuals whose relative mass changes were measured on at least three occasions (oneway ANOVAs or regressions: all $P>0.11$). The mean relative mass change of 15 individuals which were measured on at least five occasions varied between a loss of 0.47g/day and a gain of 0.52g/day, but there was no evidence that it varied consistently between individuals (oneway ANOVA: $F_{14,90}=0.28$, $P=0.99$). These results remained unchanged if measurements obtained from Spring snow spells were omitted.

8.3.9 Masses of birds on balances prior to snow spells

Individuals may have different optimum reserve levels depending, for example, on their ability to find food under worsening weather conditions or their overall ability to avoid predators. Poor foragers, given the opportunity, may maintain higher than average energy reserves, while birds with a higher than average chance of predation (e.g. through being forced to feed singly or peripherally) may choose to be leaner than average. In this section I assume that Snow Buntings are able to forage most easily under snow-free conditions and that their body-masses at the beginning of a spell of snow are therefore most likely to reflect their optimum stored energy reserve levels (as measured by body-mass). I then test for differences in the body-masses of birds at the start of snow spells in relation to various individual attributes.

The daily mass of an individual Snow Bunting visiting the electronic balances was calculated as the mean of all its mass readings in a day (each reading weighted by the deviation on the balance due to wind - see **8.2.2**). The mean time of these observations was also calculated in the same way. The daily mass was then standardised to the equivalent mass of an average-sized male (see **8.2.1**). Next, I worked out, for each day, the average of all individuals' mean times of balance readings, and corrected their daily masses to this time using an estimate of the hourly rate of mass gain. As the hourly rate of mass gain varied within the winter (see **8.3.5** and **Fig.8.13**), I used either the mean of hourly rates of mass gain for those days on which it was actually measured (see **8.3.5**), or, if this was unavailable, the expected hourly rate of mass gain calculated

from **Fig.8.13**. Finally, I calculated the residual mass of each individual, i.e. its adjusted mass in relation to the mean of the adjusted masses of all birds weighed that day. Only the first value of residual mass for an individual in a bout of balance readings was used - 57% (n=251) of these occurred on the first day of balance readings in each snow bout.

I then examined residual mass in relation to age, sex, experience, breeding status, dominance status and size. Residual masses were initially treated as a single sample without separating them into snow bouts and so some individuals contributed more than once to the analysis. As a result, I found that breeding status was the best overall predictor of residual mass: winter immigrants were heavier than local breeding birds (oneway ANOVA: $F_{1,249}=18.8$, $P<0.001$). However, when the snow bouts were examined individually, breeding birds were only consistently lighter than winter immigrants in snow bouts beginning in March. During winter (December and February) there was no consistent difference in residual mass between breeders and winter immigrants (**Fig.8.14**). I interpret this as evidence for premigratory fattening of the winter immigrants. Hence, I therefore repeated the tests, but looked for differences in residual mass between individuals in the Early/Mid Winter period alone.

I again initially treated all the residual masses in Early/Mid Winter as one sample, but could find no significant differences in residual mass between juveniles and adults, males and females, experienced and naive individuals, dominants and subordinates, or large and small birds (oneway ANOVAs or regressions, all $P>0.66$). This result remained unchanged if the mean residual mass of individuals was used. However, although I could not ascribe variation in residual mass to an individual's attributes or behaviour (age, sex, dominance, etc.), there was evidence for consistent individual variation in residual mass: for individuals whose residual mass was measured on at least three occasions in Early/Mid Winter, mean residual mass varied between -2.5g and 3.8g (n=28; oneway ANOVA: $F_{27,86}=2.42$, $P=0.001$). The range of this variation is more than one and a half times the difference expected between the sexes. Therefore, given that mass had already been standardised to that of an average male, the variation is unlikely to be due simply to individual differences in shape or lean mass.

8.3.10 Comparison of masses of birds caught and those on balances

Although prior site experience did not appear to influence body-mass or fat reserves of trapped Snow Buntings (**8.3.4**), an effect of experience may not have been found if experienced birds tended to avoid the trapping sites *except when underweight*. Indeed, some 74% of Early/Mid Winter weighings from birds captured on Cairn Gorm were from birds which had not previously been caught there, while the remaining 26% were biased towards birds with low prior site experience (**Fig.5.3**). Similarly, I could find no evidence that prior site experience influenced either body-mass or mass changes of birds visiting the electronic balances (**8.3.5, 8.3.8 & 8.3.9**), but in this case the data set was biased towards *experienced* birds. This was primarily because I could not ascribe sets of balance readings to individual unringed (and by definition

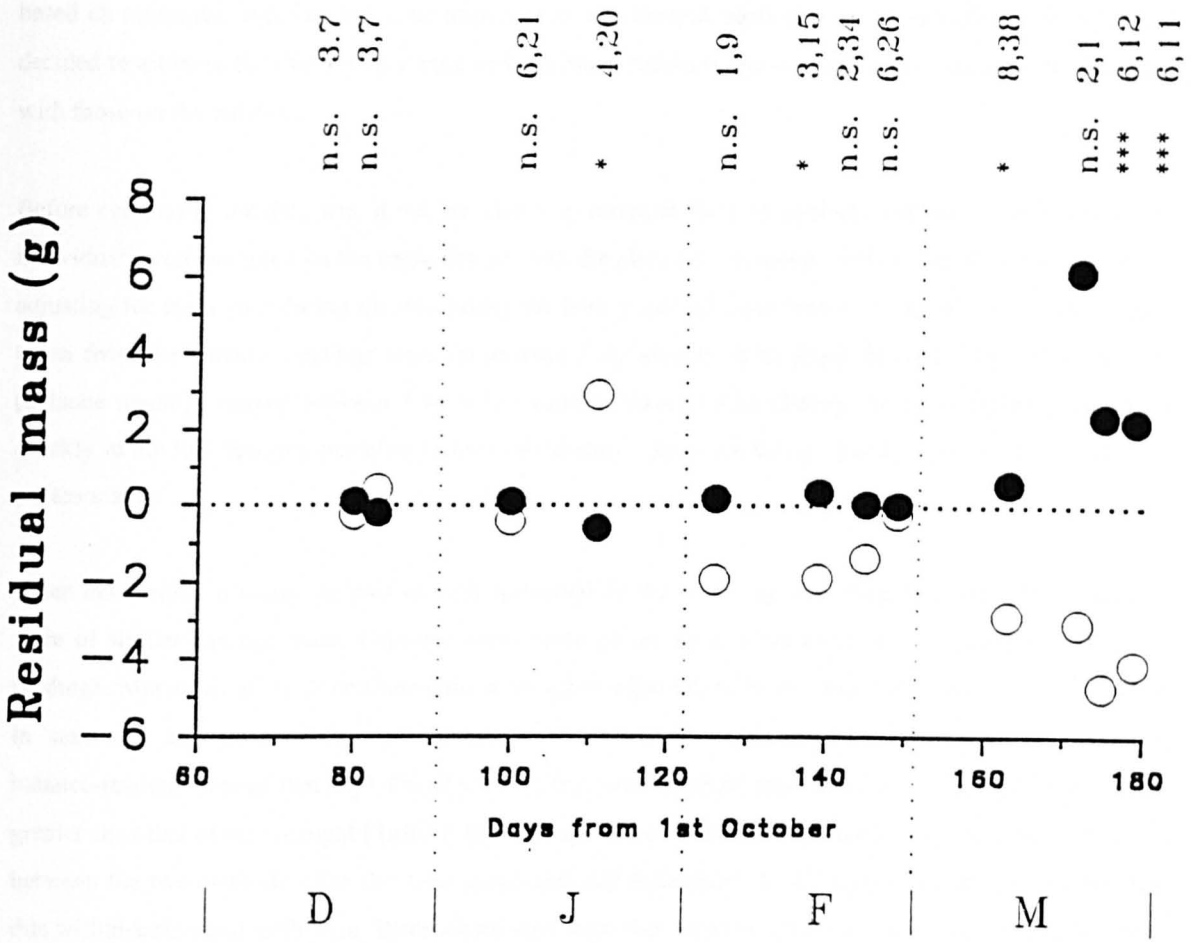


Fig.8.14. A comparison of the mean residual masses of locally breeding (open circles) and winter immigrant Snow Buntings (filled circles) during the non-breeding season. *See text for calculation of residual mass. The numbers above the figure are the number of local breeders (before comma) and winter immigrants (after comma) contributing to each pair of points, while the asterisks indicate significance (* = P<0.05; *** = P<0.001). Winter immigrants were consistently heavier than local breeding Snow Buntings only during the Spring samples.*

inexperienced) birds with certainty, and hence could not use the data from such birds. Secondly, however, marked individuals which had no site experience in previous winters contributed only 12% of the readings from the electronic balances, hence reducing the power of any statistical tests. As the contribution of experienced birds to the electronic balance data set was much higher than their contribution to the data based on trappings, and data based on trappings of experienced birds may be biased towards lean birds, I decided to estimate the role of experience on body-mass indirectly by comparing the masses of birds caught with those on the balances.

Before comparing the data sets, it was necessary to calibrate the two methods with each other. Only four individuals were weighed on the same day on both the electronic balances and as a result of capture. After adjusting for mass gain during the day (using the hourly rate of mass gain as in **8.3.9**), estimates of mass taken from the balance readings were on average 1.1g greater than those derived from captured birds (balance readings ranged between 1.4g below capture mass to 2.8g above). As birds probably lost mass quickly in the first few minutes after capture (defecation, etc. - see **8.3.2**), this difference was perhaps not unreasonable.

I then determined whether samples of birds measured on the same day, but using the different techniques, were of similar average mass. Captures were made on six days when there were simultaneous balance readings. Masses of all birds on these days were again adjusted, as in the previous section, for differences in sex, size and time of day (all masses were standardised to average-sized males at the mean balance-reading time on that day). On all six days the mean adjusted mass of birds visiting the balances was greater than that of birds caught (**Table 8.5**). In all six cases the difference exceeded the average difference between the two methods when the *same* individual was reweighed (1.1g), and averaged 2.5g greater than this within-individual difference. Birds which were captured therefore generally appeared to be lighter than those using the balances.

An alternative method of relating the mass of birds weighed on the balances with capture masses, was to compare the mean mass of birds on balances with their expected mean mass, calculated from the Cairn Gorm winter mass curve (**Fig.8.7**). Mean balance masses of individuals were again standardised to those of average-sized males. However, on this occasion, to allow direct comparison with the curve, they were also adjusted to the estimated mass at noon (again using hourly rates of mass gain as calculated in **8.3.9**; using the fixed rate of 0.39g/hour from **Table 8.1** gave similar results). As masses on consecutive days are obviously not independent of each other, I only included the first day of each bout of balance readings in the analysis. The mean noon readings from birds on the balances were all higher than the curve (**Fig.8.15**). On average, they were 2.7g (±1.4g s.d.) greater than expected. This is slightly less than the 3.6g estimated from simultaneous daily balance and capture masses above, but again indicates that captured birds probably averaged leaner than birds visiting the electronic balances.

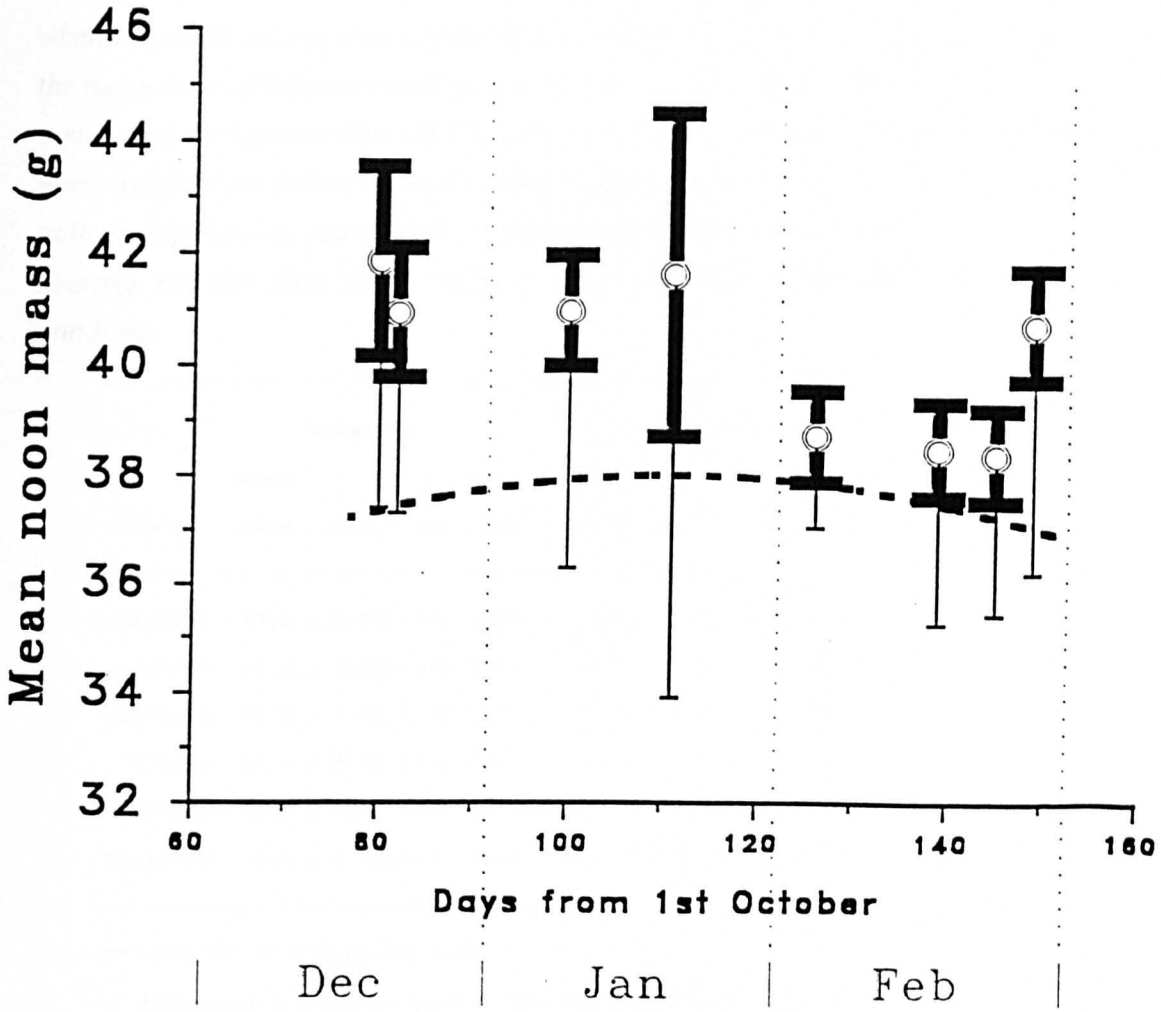


Fig.8.15. The mean mass of Snow Buntings on the first day of balance readings during eight Early/Mid Winter bouts of balance readings, in relation to their expected mass calculated from captured birds (i.e. the curve; see Table 8.1 **&** Fig.8.7**).** *The mass of birds on balances was standardised to those of average-sized males at noon. Shown are the mean, 95% confidence interval for the mean (thick bar), and the lower limit to the normal distribution (narrow bar) below which only 2.5% of observations were expected to fall. Sample sizes contributing to each mean are (left to right) 7, 10, 23, 7, 4, 14, 12 & 21 mass readings of individuals.*

Table 8.5. A comparison of masses of birds weighed on the electronic balances, and those of different birds captured on the same day. *The mean mass of all individuals, whether on the balances or captured, was standardised to that of average-sized males at the mean time of balance readings for the relevant day. For captured birds the mean time serves only to indicate that catches were both before and after the mean time when birds were weighed on balances, and therefore that error involved in the estimation of mass gain during the day was unlikely to explain my results. Birds coming to balances were on average heavier than those trapped, even after accounting for loss of mass during handling.*

	Balances:				Captured:						
Date	Mean mass	s.d.	(n)	Mean time	Mean mass	s.d.	(n)	Mean time	Diff. a	t	P
28/2/91	40.9	± 1.8g	(23)	1648	38.8	± 2.1g	(24)	1030	1.0g	1.71	
1/3/91	40.0	± 2.0g	(25)	1200	36.6	± 1.9g	(9)	1345	2.3g	2.57	*
22/3/91	38.2	± 5.8g	(3)	1300	36.6	± 4.8g	(6)	1000	0.5g	0.12	
9/1/92	42.6	± 2.0g	(20)	1136	36.8	± 1.6g	(7)	1615	4.7g	5.41	***
13/3/92	42.0	± 4.8g	(38)	1136	36.3	± 3.2g	(17)	1315	4.6g	3.43	***
23/12/92	39.0	± 4.6g	(3)	1006	35.7	± 1.8g	(9)	1515	2.2g	0.91	

*** P<0.001, ** P<0.01, * P<0.05

a **Difference is the mean mass on balances minus the mean mass of captured birds *minus 1.1g* (estimated loss as a result of capture - see text).**

Both comparisons of mass of trapped birds versus those measured on electronic balances indicated that the latter average heavier. Experienced birds predominated in the data set from the balances, but not in captures, indirectly suggesting that the difference in mass between the sampling techniques was a result of the greater site experience of birds measured on the electronic balances. Other possible explanations of this result are discussed in **8.4.4**.

8.3.11 Mass differences between sites

Did Snow Buntings at high altitude sites struggle to meet their energy requirements as a result of more difficult foraging conditions, or did they respond to a more variable food supply by maintaining greater average energy reserves? This section compares the body-masses of birds trapped at different altitude sites

in North-east Scotland.

To control for seasonal variation in mass, I grouped catches within months and standardised masses to noon masses using an average rate of hourly mass gain for each month (calculated from **Fig.8.13** as the rate of hourly mass gain on the middle day of the month; similar results were obtained if the hourly rate of mass gain was assumed to be fixed at 0.39g/hour). The masses were further standardised to their equivalents if all birds had been average-sized males. Data from catches at coastal sites were only available from January and February, so comparisons with catches in upland areas were made only during these months.

Considering each mass as an independent datum, regressions of the adjusted noon mass on the principal component Altitude (see **4.2**) were highly significant (January: r_{951}=0.53, P<0.001; February: r_{879}=0.22, P<0.001). A similar result was obtained if catch means, as opposed to individual masses, were used (**Fig.8.16**), or if catch means were analysed with respect to wintering habitat (**Table 8.6**): coastal wintering Snow Buntings were lighter than those wintering inland, especially those on the ski areas. Interestingly, the regression slope between mass and Altitude was steeper in January than February (**Fig.8.16**; MANOVA, interaction between Altitude PC and month: $F_{1,75}$=6.15, P=0.015).

Table 8.6. Mean of average masses of Mid Winter catches of Snow Buntings at coastal, inland farmland and upland sites. *Masses are standardised to those of average-sized males at noon. Only catches of five or more birds were included.*

	Mean (g, ± s.d., n) of average mass of catches in:	
	January	February
Coastal a	34.6 ± 0.7 (7)	35.8 ± 0.6 (5)
Farmland b	35.9 ± 2.1 (5)	36.6 ± 1.1 (8)
Upland c	37.7 ± 1.4 (30)	37.0 ± 1.0 (24)
oneway ANOVA	$F_{2,39}$=15.22 P<0.001	$F_{2,34}$=3.74 P=0.03

a Newburgh, Balmedie and Rattray

b The Cabrach and Corgarff

c Cairn Gorm, The Lecht and Glen Shee

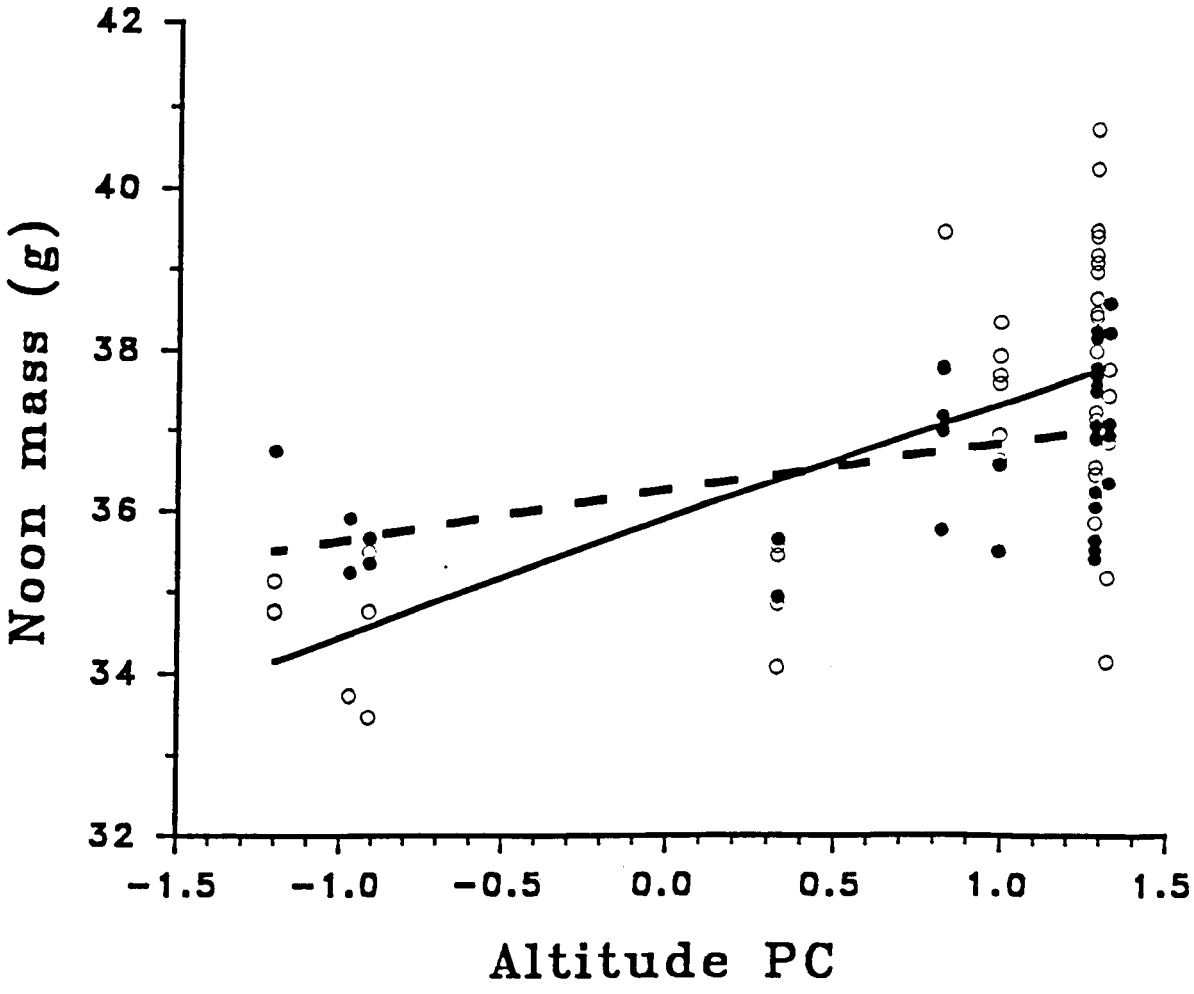


Fig.8.16. Average mass of Snow Bunting catches plotted against the principal component Altitude. *Catch masses were standardised to that expected if all birds were average-sized males at noon. Only catches of five or more birds were included. January catches are represented by the hollow circles and solid line, February catches by filled circles and the hatched line. Noon mass increased with Altitude in both months (January: $r_{40}=0.68$, $P<0.001$; February: $r_{35}=0.48$, $P=0.003$), but the slope was significantly steeper in January (see text for details).*

8.3.12 Changes in mass in spring

8.3.12a Winter immigrants

This section describes the increase in body-mass observed in winter immigrant Snow Buntings during March and April as they fattened prior to spring migration. Data were available from Cairn Gorm, Glen Shee, The Lecht and Corgarff, totalling 1084 birds thought to be winter immigrants. Masses were adjusted to that expected at noon using an hourly mass gain function estimated from **Fig.8.13**. Age/sex categories were treated separately. Juvenile females and adult males showed significant increases in mass with date, and the trend was similar and near significant in adult females (regression lines shown on **Fig.8.17**: juvenile females, $r_{489}=0.15$, $P<0.001$; juvenile males, $r_{196}=0.05$, $P=0.51$; adult females, $r_{286}=0.11$, $P=0.056$; adult males, $r_{105}=0.27$, $P=0.004$). The same trends were apparent if mean catch masses of a given age/sex category were used (only catches with at least five of the relevant category were used - indicated by points on **Fig.8.17**). Across all age/sex categories there was a significant increase in both mean mass and the coefficient of variation of mean mass with date (Combined Probability Tests, combining the four age/sex regressions: for mean mass, $X^2_8=15.6$, $P<0.05$; for c.v., $X^2_8=22.9$, $P<0.01$).

8.3.12b Local breeders

Unlike winter immigrants, local breeding Snow Buntings had no need for premigratory fattening. Therefore I predicted that they would continue to lose mass throughout the spring period. In total, 54 measurements were obtained from 37 individual local breeders on the ski areas (mostly Cairn Gorm) during March, April and May. After standardising these to the equivalent body-masses of average-sized males at noon, I plotted mass against spring date. As expected, local breeding birds continued to lose mass as the breeding season approached (**Fig.8.18**; $r_{52}=-0.32$, $P=0.02$). Seventeen local breeding males weighed during the summer (June to August) averaged even lighter (33.7g ± 2.2g s.d.).

8.4 DISCUSSION

8.4.1 Rates of mass change and fasting capacity

The calculated rate of overnight mass loss was only half of the rate of mass loss of birds held captive during ringing (0.43g/hour), but slightly higher than the rate of mass loss of an injured immobile individual. In fact, because the rate of mass loss of this injured individual decelerated with time (**Fig.8.5**), the calculated overnight mass loss was very similar to the injured bird's rate of mass loss in its first 24 hours in captivity. The close similarity between the resting rate of mass loss of this injured bird and the calculated resting rate of mass loss therefore indicates that the seasonally-adjusted hourly rates of mass gain whilst feeding (**Table 8.3**) may be reasonably accurate. Using these figures, overnight mass loss would average

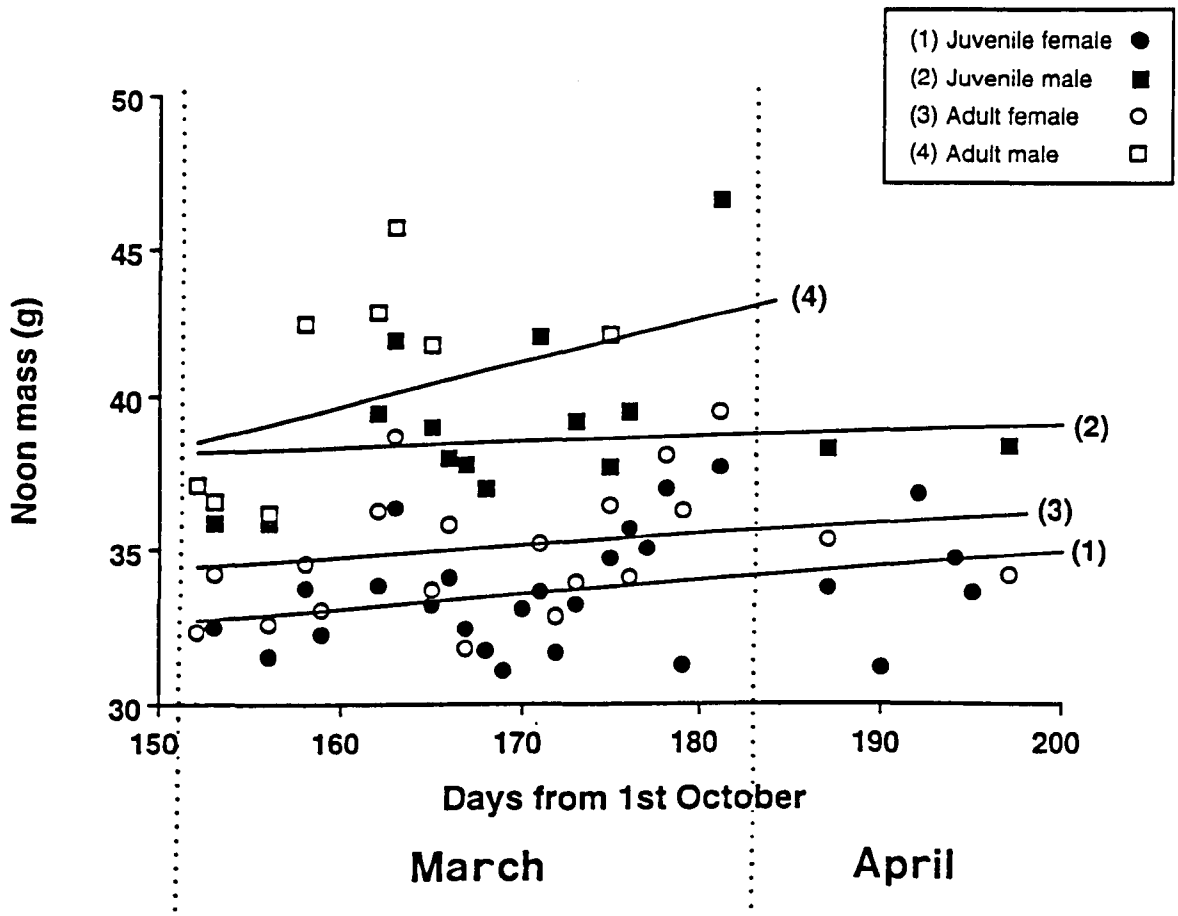


Fig.8.17. Mass of Snow Buntings (adjusted to noon) in relation to spring date. *Points indicate the mean mass of Snow Buntings of a particular age/sex category on days when at least five were measured. The regression lines are for all Snow Buntings of a given age/sex category caught in spring and are shown over the range of days for which data was available (see text for significance levels).*

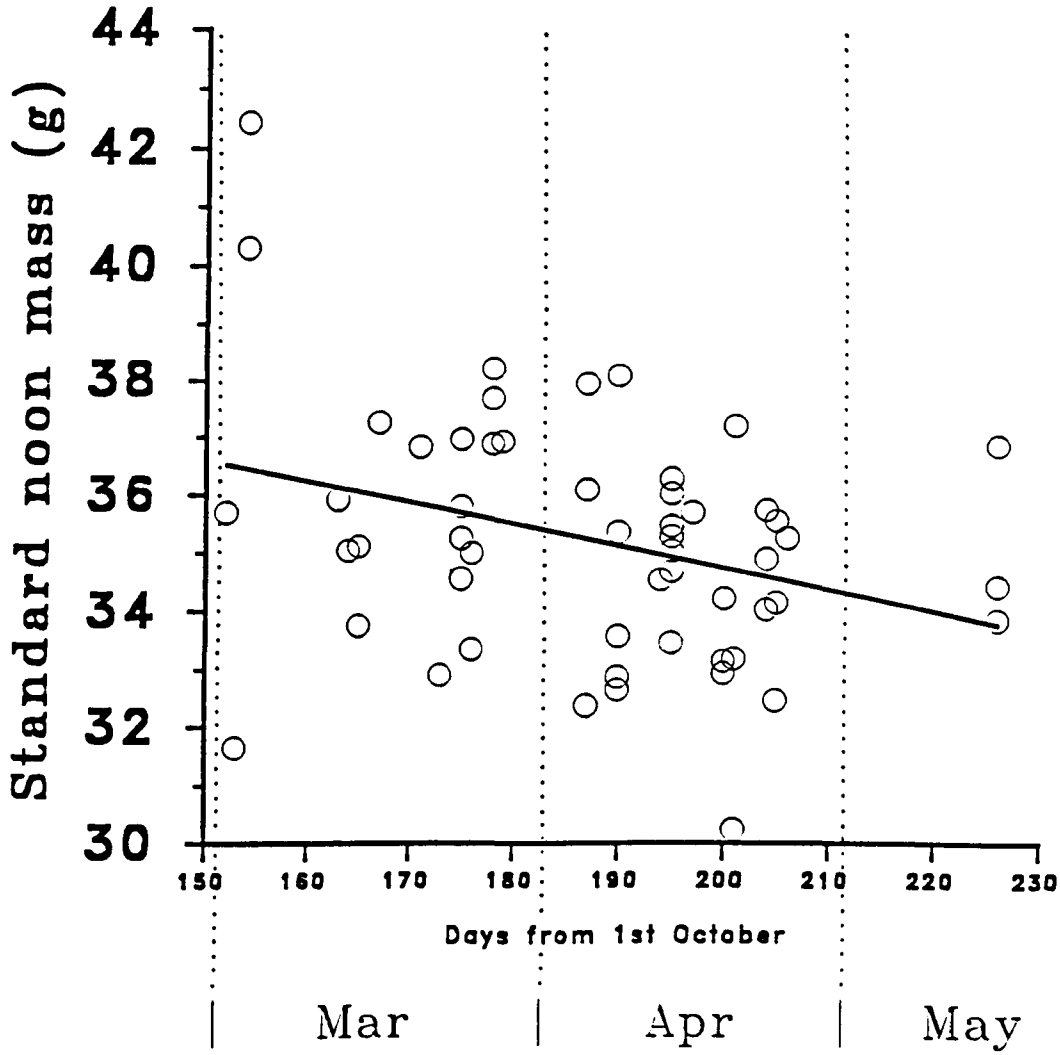


Fig.8.18. Mass of local breeding Snow Buntings in relation to date in spring. *Local breeders became lighter as spring progressed.*

about 7-10% of the dusk body-mass, similar to the 9.2% found in an ecologically similar species, the Snow Finch (Heiniger 1991).

Assuming, as seems likely, that the injured individual eventually died of starvation rather than its injuries, its mass at death gives us some idea of starvation mass and, along with rates of resting mass loss, allows me to calculate approximate fasting endurances of wintering Snow Buntings. The injured bird weighed 25.6g at death, and since it was a juvenile female with a wing-length of 103mm, it can be calculated (from **Table 8.1**) that average-sized females would starve at about 26g and an average male at around 30g. Banks *et al.* (1989) calculated the mean lean weight of North Scotland Snow Buntings from the average masses of birds with low fat scores, obtaining estimates of 28.9g for females and 33.0g for males. These values can be compared to the minimum masses of Snow Buntings in Scotland in summer and autumn (local breeders only) when the optimal level of stored energy reserves would be expected to be lowest, as in other passerines (reviewed by Witter & Cuthill 1993, see also Holmes 1976). The lightest female weighed 28.1g and the lightest male, an unusually small individual, weighed 29.9g (n=163 & 139 individuals, unpubl. data). These masses are similar to my predicted starvation masses, but lower than the mean lean weights calculated by Banks *et al.* (1989). Furthermore, only two out of the 2193 individuals weighed during Early/Mid Winter were less than my predicted starvation mass, compared to 81 (3.7%) below Banks *et al.*'s (1989) mean lean weight.

Fig.8.19 shows the distribution of expected fasting endurances of the Early/Mid Winter trapped sample using my estimate of starvation mass. The mean fasting endurance was 34 hours (± 12 hours s.d.) at inland sites (median=33 hours). Overall, 79% of birds could have fasted for more than a day, but only 10% for more than two days. If individuals conformed to the predicted rate of mass gain for the remainder of the day when they were trapped, I would have expected only 14 (0.6%) to have starved overnight. These may have been able to take greater feeding risks to increase their rate of mass gain during the remainder of the day (as suggested by Loria & Moore 1990 to explain different microhabitats and behaviours used by lean versus fatter migrant Red-eyed Vireos). However, only 27% of individuals could have survived two nights and the intervening day without feeding. Most Snow Buntings therefore probably need to feed each day to survive.

The fasting endurance of Cairn Gorm Snow Buntings is probably less than that of another ground-feeding finch, the Brambling, which Jenni & Jenni-Eiermann (1987) calculated could fast for several days. Bramblings may be particularly at risk of losing mass when snow covers their winter food supply of fallen Beech mast. Vincent & Bedard (1976) noted that Snow Buntings from Quebec, Canada, held captive in outdoor aviaries in winter and accidentally deprived of food, survived for 2-3 days "without apparent ill affects". This is appreciably longer than I have calculated for average winter mass Snow Buntings in North-east Scotland, possibly because of the need to endure longer and/or harsher spells of bad weather in Canada.

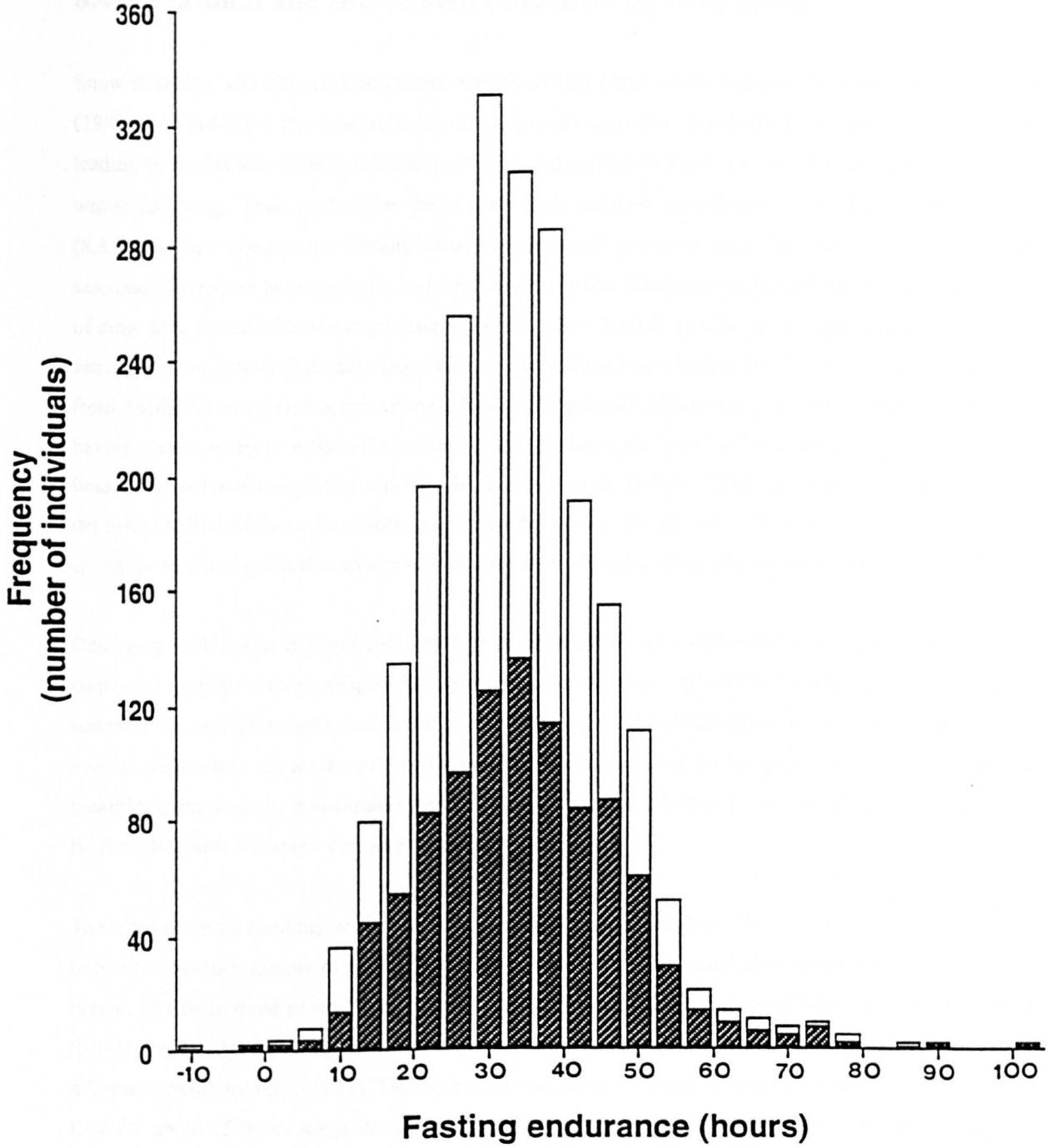


Fig.8.19. The frequency distribution of estimated fasting endurances of Early/Mid Winter Snow Buntings caught at Cairngorm (filled bars) and other inland sites (blank bars), assuming that mass is lost at 0.21g/hour whilst resting.

8.4.2 Seasonal and site-related influences on body-mass

Snow Buntings wintering on Cairn Gorm appear to exhibit true winter fattening as defined by Lehikoinen (1987), i.e. excessive overcompensation of daily mass gain over overnight mass loss up to mid-winter leading to an increase in daily minimum, average and maximum mass, and the opposite pattern from mid-winter to spring. Their mid-winter dawn mass peak occurred considerably later than the shortest day (**8.3.7**), perhaps because the severity of winter conditions generally peak after this date. Assuming that seasonal differences in temperature and other environmental conditions have only marginal effects on rates of mass loss, the additional energy reserves would allow them to fast for about eight hours longer in late January (when fattest) than early December, or about three hours longer than in late February (calculated from **Table 8.4** and a fasting rate of mass loss of 0.21g/hour). Alternatively, of course, the importance of having greater reserves at these times could be that the bird could survive for longer periods when food was inadequate but not completely unavailable. Lehikoinen & Hakala (1988) showed that Finnish Dippers deposited sufficient fat to give them an extra 4-6 hours daylight survival time in mid-winter. This estimate is similar to mine, given that energy will be used more quickly whilst attempting to feed.

Consistent with longer daylight feeding hours and less chance of severe weather, masses of non-migrants continued to drop in spring (**Fig.8.18**). However, males continued to maintain a significant fat reserve in summer, i.e. enough to withstand a fast of about 18 hours. The maintenance of such an energy reserve, even at presumably the most nutritionally benign time of year, may be influenced by variance in feeding conditions, particularly mid-summer snowfalls which are not infrequent even in Scotland at a southerly limit of the Snow Bunting's breeding range (pers. obs.).

The mass of Snow Buntings at high altitude sites was greater than that of birds on the coast (**8.3.11**). The only other Scottish sample of winter Snow Bunting masses, from coastal sites in northern Scotland, gave masses similar to those presented for coastal birds above (converting data from Banks *et al.* 1989, Table 4, to that for average-sized males as above, mean mass = 34.6g, n=1189 January/February masses, no allowance made for time of day). The extra mass would have allowed high altitude birds to survive without food for about 15 hours longer than their coastal counterparts in January, and about six hours longer in February (based on calculations using the resting rate of mass loss in **Table 8.3**). Ambient temperature and other environmental differences between sites may reduce this advantage. As with latitudinal trends (Nolan & Ketterson 1983), the reason why greater energy reserves are required at higher altitudes is probably climatic. The probability of suffering poor feeding conditions, as a result of ice- or snow-cover, will increase with altitude, just as it does with latitude and in mid-winter. Extra energy surpluses reduce the likelihood that an individual will starve during a winter snowstorm. They may also be adaptive if migration away from bad conditions is necessary, although the distance between high and low altitude sites in North-east Scotland is short (no site was further than 60km from the coast).

The average difference in body-mass between high altitude and coastal Snow Buntings was more extreme in January than February (**Table 8.5**). This may reflect a greater mid-winter peak in body-mass at high altitude sites - short daylength and harsher weather in January may have more than an additive influence. Banks *et al.* (1989) could find little evidence for mid-winter fattening at several coastal sites in North Scotland, supporting the argument that mid-winter fattening is mainly required in extreme climates (see similar phenomenon in northerly versus southerly populations of Meadow Pipits studied by Hotker 1989). Although no mid-winter peak was seen at Glen Shee or The Lecht, this may have been a result of the irregular baiting and catching regime. Snow-cover on the coast, even in North Scotland, is far less frequent and birds may be able to maintain their optimal energy reserve strategies more effectively. Interestingly, coastal birds may even have been heavier in February than January (**Table 8.5**), perhaps to allow them to move inland to fatten prior to migration.

8.4.3 The influence of weather on mass

Severe weather can both (i) promote fattening because birds may perceive an increased risk of starvation (e.g. Nolan & Ketterson 1983, Jenni & Jenni-Eiermann 1987), and (ii) cause loss of condition when the prevailing weather prevents daily energy intake from balancing or exceeding expenditure (e.g. Fox *et al.* 1992). Similarly, loss of mass could be either forced (severe weather causing an excess of energy use over energy gain), or voluntary (shedding of excess energy deposits when conditions were perceived to be ameliorating). The effect of severe weather on mass change may also vary within the winter because the ratio of daylight to darkness hours changes considerably. Moreover, changes in population size also occur as a result of snowfalls (**5.3.5**), hence affecting access to food. Prediction of how mass would be affected by prevailing weather is therefore extremely complicated, and the low amount (18%) of variation in mass residuals explained by weather variables was not unexpected.

There was considerable daily variation in 24-hour mass changes as recorded on the electronic balances (**8.3.8**), indicating that birds gained mass on some days and lost it on others and that these changes tended to be synchronised among population members. However, the low number of pairs of days when sufficient birds were weighed prevented me from finding any significant effect of weather on changes in mass. A much larger sample, perhaps including some interaction between weather variables, is required, and adequate consideration of the effects of day-length and population size would also be necessary.

A more extensive sample of masses of *caught* birds was available, and allowed some recognition of the factors causing birds to lose mass. Severe weather would be expected to promote fattening if birds could follow their optimal energy reserve strategies (Lima 1986, McNamara & Houston 1990), but my finding that birds were lighter during periods of snow-cover (**8.3.3**) suggests that they struggled to find sufficient food at these times. Although the differences in mass between the various categories of weather conditions were small (less than 2g - **Figs.8.8, 8.9 & 8.10**), and the mass deficit did not appear to accumulate between

days (**Fig.8.10**), they may still have been important because the optimal strategy may have been to *fatten* on these days, and emigration of the lightest birds may have been occurring (see **9.3.3**). Meltofte (1983) noted a similar severe weather decrease in mass (1.5g) of male Snow Buntings in East Greenland in April, but longer daylight hours may have reduced the effect by May.

8.4.4 Individual differences in energy reserves

Most of the analyses in this chapter control for the difference in body-mass between genders by considering that the mean difference in mass between sexes, after controlling for other variables (**Table 8.1**), represents the difference in the average lean mass of the sexes. This assumes that, on average, both sexes were similar amounts heavier than their lean masses when weighed. The results of the analysis of within-catch FAT DEVIATIONs (**8.3.4**) suggested this may not be the case. Males tended to have higher fat scores than females, suggesting that their energy reserves (and hence fasting endurances) were correspondingly larger. Moreover, the average mass difference between genders tended to increase as fat score increased (**Fig.8.1**), indicating that for a given fat score the surplus energy available to males was higher than that for females (assuming fat increased proportionately with mass). Of course, the larger-bodied males may have to use this energy more quickly in absolute terms than females, but in proportionate terms they may be more economical (Kendeigh 1970, Calder 1974, Ketterson & Nolan 1976).

On average, males were approximately 4.1g heavier than females in the Early/Mid Winter samples from Cairn Gorm (2.78g + 0.2g x wing-length difference between sexes, see **Table 8.1** & **3.3.3**). Taking the observed distribution of fat scores in this sample, assuming the distribution of fat scores was identical in the two sexes, and using the observed difference in mass for a given fat score as presented in **Fig.8.1**, I would have expected males to have been only 3.7g heavier than females in this sample. On average, males therefore seem to have approximately 0.4g more surplus mass than females, and this may be largely associated with extra fat deposits.

When standardising individuals to their equivalent body-masses if they were average-sized males, I always used the parameters given in **Table 8.1**. Therefore the 4.1g difference between the sexes was assumed to be wholly a result of morphological variation rather than wholly or partially due to intersexual differences in energy reserves. As I have just explained, this may not be the case. However, it should make little difference to any of the analyses, because the samples were not biased with respect to sex. The main exception, however, was the comparison of differences in mass between sites because females were proportionately commoner at lower sites (**4.3**). Because the 4.1g correction was too generous, the increase in body-mass (and hence energy reserves) with Altitude is likely to be even more marked than the results suggest.

Although no difference in FAT DEVIATION was found between age groups (**Fig.8.12**), MASS

RESIDUALs and MASS DEVIATIONs were greater in adult females than juvenile females (no disparity found in males). No differences between birds of different experience or dominance were noted in these tests. However, an effect of experience may not have been found if experienced birds tended to avoid the trapping sites *except when underweight*. Indeed, the greater mass of birds measured on the electronic balances (**8.3.10**) suggests that experienced birds were heavier than inexperienced individuals, because experienced birds predominated on the balances while mostly naive birds were trapped.

Of course, other differences between the data sets could have influenced this result. The most obvious alternative explanation is that trapped birds may still have been wary of nets even though few may have ever seen other birds get caught. But to my eye the balance set-up also appeared unnatural and potentially dangerous (cables, boards, wind baffles, etc.). Also, little effort was made to catch birds if they did appear particularly wary, because this was time consuming and catches were consequently small. Another distinction between the data collection methods was the type of food supplied and the way it was delivered. But food was presented over a larger area at the trapping sites than on the two small balance tops, so getting access to food should have been easier for trapped birds. In conclusion, the difference in mass between electronically weighed and trapped birds was substantial (about 1.5-2.5g on average, after allowing for mass loss during handling) and not convincingly explained by differences in methodology, suggesting that differences in experience between birds contributing to each data set were also involved.

The difference in mass between electronically-weighed birds and birds caught the same day was 3.6g (**Table 8.5**). The difference between the masses of electronically-weighed birds on the first day of snow-bout weighings and the average seasonally-adjusted mass of caught birds was only 2.7g (**8.3.10** & **Fig.8.15**). This was surprising. I expected the difference between samples to be greater from the latter comparison because the data I used for the electronically-weighed sample was taken mainly from the start of snow-bouts (when birds should have had most opportunity to fatten to the seasonal optimum, see **8.3.9**). In contrast, the seasonal mass curve included many birds weighed during the course of snow-bouts (when they tended to lose mass, **8.3.3**). Hence, the difference between sampling techniques should have been at a maximum. The opposite result is possibly a consequence of the conundrum posed in the previous section - birds want to fatten in bad weather but in some cases can't. Experienced birds, mainly visiting the electronic balances, were usually able to at least maintain mass (average daily mass change=+0.14g, **8.3.8**), whilst inexperienced birds visiting the catching site were not (**8.3.3**).

This differential reaction to weather conditions was the only one observed during this study. There was little evidence that weather conditions caused a change in the relative mass or fat reserves of one gender, age or dominance group relative to the other (**8.3.4**). However, this may not have been because there was no difference between groups, but because particularly light individual juveniles or females tended to leave the site (see **9.3.3**).

The tendency for individuals to be at a consistent mass relative to other individuals at the start of snowy periods (**8.3.9**) may be indirect evidence that they each have optimal energy reserve strategies which they can return to, if necessary, between spells of snow. Although there was no evidence that the hourly rate of mass gain or the 24-hour mass change varied consistently between individuals, fewer data were available on these aspects, 'rogue' readings may have been more influential, and the relative differences between individuals may have been less dramatic. It is therefore still quite possible that some birds may have shed reserves at the end of snow bouts, while others needed to make up lost mass.

Are females, especially juvenile females, and inexperienced birds lighter because they are less able to accumulate fat reserves than their counterparts, and/or more prone to lose reserves when the weather worsens? Several studies have indicated that the mass of dominant or adult birds increases in relation to that of subordinate or juvenile birds when feeding becomes more difficult (Swingland 1975, Baker & Fox 1978, Jenni & Jenni-Eiermann 1987, Wagner & Gauthreaux 1990). Dominant individuals may be more able to maintain a consistent body-mass over the course of the winter (Peach *et al.* 1992, Ekman & Lilliendahl 1993) than subordinate birds. Extra fat deposits presumably give male, adult and experienced Snow Buntings a greater chance of surviving long periods when feeding is difficult or impossible. It is also just possible that adult males do not have *greater* fat deposits than juvenile males because they do not need them. They are more efficient foragers (**6.3**) and are perhaps less limited by prevailing conditions. Hence, the benefits of extra fasting endurance for adult males do not match the extra costs of carrying excess fat.

There are also two possible reasons why females and birds with little site experience might *choose* to maintain lower energy reserves than their counterparts. Firstly, these birds may be more vulnerable to predation by feeding in smaller flocks, or on the edges of such flocks, or at times when predation risk is higher (see **6.3.4**). They may therefore increase their ability to avoid predators by maintaining lower body-mass (as demonstrated experimentally by Witter *et al.* 1994). Secondly, emigration during bad weather may be so commonly necessary, due to limited feeding opportunities, that the cost of transporting the extra mass between sites becomes inhibitory to fattening (see also Senar *et al.* 1992a for a similar discussion to explain the difference in mass of resident and transient Siskins). Experimental studies of birds on an ad libitum diet are necessary to distinguish between these possibilities.

8.4.5 Spring fattening

The rates of mass gain in spring shown in **Fig.8.17** are not those of individual birds, but those of the population visiting the catching sites. The situation is complicated because two races of Snow Buntings overwinter in Scotland and western Europe (Banks *et al.* 1991a, Jukema & Fokkema 1992, Smith in prep.), and these probably have different migratory timetables (unpubl. data). Closer inspection of **Fig.8.17** shows rapid mass increases until mid-March in adult males and until late March in juveniles and females, followed by lower masses thereafter. This probably represents an earlier pre-migratory fattening period and

departure of birds of the Icelandic race *insulae*. The remaining birds are mainly of the *nivalis* race, destined to leave for Greenland or Scandinavia in April. From recaptures of birds caught twice in the same spring, Banks *et al.* (1989) calculated that North Scotland Snow Buntings fattened by at least 0.30g/day. This is considerably higher than the population rates depicted in **Fig.8.17**. On average, adult males fattened earlier than females, allowing them an earlier return to the breeding grounds (as observed in East Greenland by Meltofte 1983).

An increase in the coefficient of variation of body-mass during the spring probably indicates that the proportion of birds which were actively fattening increased as the spring progressed. Banks *et al.* (1989) claimed that the duration of premigratory fattening was between 15 and 20 days, so many birds measured in early March would still not have begun to fatten. I calculated an individual's fat load as:

(total mass minus lean mass)/lean mass

(as in Banks *et al.* 1989). Assuming that less than 10% of birds caught were actually ready to migrate, and that the mean mass of the top 10% of birds was a fair reflection of the departure mass, the mean fat loading on departure was in the region of 42-56% (depending on whether Banks *et al.'s* mean lean mass or my starvation mass is used). The heaviest bird would have had a fat load of 68-85%. These values are far higher than those given by Banks *et al.* (1989), and would allow Snow Buntings in the Cairngorms to reach breeding areas in Iceland, and possibly even Greenland, directly. This is consistent with the lack of spring movements of Snow Buntings between the Cairngorms and the North Scottish coast (**5.3.6**), despite the large amount of trapping conducted in both areas.

8.4.6 Size difference between the sexes

Inspection of **Fig.8.2** reveals that, for a given fat score and mass, females would have a wing-length about 11mm greater than that of males. This could mean that females have relatively larger and/or more pointed wings than males. The former generally allows greater flight manoeuvrabilty, while more pointed wings give faster more efficient flight (Rayner 1988, Norberg 1989). There are several reasons why either or both of these qualities may be more important to females. Firstly, since females more often feed in dangerous situations (see **4.4** and **6.3.4**), greater maneouvrability may be relatively more important in reducing their vulnerability to predators. Secondly, females are more often found in the southern parts of the wintering range (Banks *et al.* 1991a), necessitating a longer migratory flight, and hence a greater need for flight efficiency (Mulvihill & Chandler 1991 postulated similar reasons to account for differences in wing shape amongst Dark-eyed Juncos). Thirdly, for similar reasons, efficient flight may be more important to females if they travel further and more frequently between wintering sites. This is supported by the work of Senar *et al.* (1994) who found that, independently of age and sex, transient Siskins had more pointed wings than resident birds. Whatever the main reason for the intersexual difference in relative wing-length between the sexes, the morphological consequences appear to be consistent with the Snow Bunting's winter ecology.

8.4.7 Methodological considerations

Given the mobile nature of some Snow Buntings (5.3), and the potential influence of snow-cover on their ability to feed, study of their mass changes during and between snow bouts and in relation to emigration would appear to offer an excellent opportunity to investigate the role that energy reserves play in winter site choice strategies. However, a number of difficulties arose which tempered both the quantity and quality of the data.

Firstly, in order to catch or electronically weigh Snow Buntings, artificial food had to be provided, otherwise birds foraged over a very wide area. As discussed previously (6.4.2), this was not necessarily a problem for some aspects of the study because food was provided in small patches, forcing birds to compete for it in a similar fashion to their competition for patchy natural food resources during snow. However, the quality of the artificial patches were probably much greater than that experienced naturally, perhaps allowing birds to meet their bad weather energy requirements more easily than they would normally do, and therefore mollifying the influence of weather on energy reserves.

However, because Snow Buntings seemed to visit the feeders in flocks, and they appeared to flush after only a small proportion of individuals had finished feeding, I speculated that at least some birds would be unable to meet their daily energy demands (see also Swingland 1975's captive Rook flock where some flock members starved because they were unable to feed when dominants were feeding, and unwilling to feed when no other birds were feeding). The only evidence for this came from the lower discrepancy between readings from the electronic balances and catch masses at the start of snow bouts compared to later. To strengthen this result would have required larger samples of electronically-weighed birds with little site experience. Perhaps a larger selection of electronic balances with different types and densities of artificial foods could have shown such differences, but the juggling act between providing too much food (therefore preventing differential mass loss) and providing too little food (thereby forcing birds to leave the site) would be difficult.

Secondly, the use of electronic balances themselves for such small birds was not ideal, especially because Snow Buntings liked to feed in the open and did not always accept visual obstructions (i.e. some wind baffles). Wind obviously affected the accuracy of the readings, so that on some days data were unusable unless the same individual had been weighed on many occasions (see 8.3.5). On the windiest days when birds visited the balances, no readings could be obtained at all. Location of the balances in a more sheltered hollow in winter 1991/92 was less successful than anticipated. The birds appeared to be unwilling to drop off a steep bank to the feeding platform in anything less than deep snow cover, perhaps because they wished to avoid situations where all-round visibilty was compromised. The occasional appearance of a Sparrowhawk during this winter may have contributed to their hesitancy.

As already mentioned, the collective flocking behaviour of Snow Buntings was essential before differential mass changes could be anticipated. Competition for feeding places on the balance platforms, although reducing the accuracy of individual readings, was considered essential. It also allowed me to make many more readings than if smaller platforms had been used. In retrospect, a larger number of smaller platforms would have been better, especially if food densities and platform choice could have been manipulated. Such a system would be more costly and time consuming to set up, but might be the best way to work with other small flocking birds.

Another problem was the speed with which the population retreated to higher ground when the weather relented (see **5.3.4**). Long periods passed without balance readings, especially in the very mild winter of 1991/92. Unfortunately, the birds then dispersed over large areas, and the balances were far from portable. It was therefore impossible to look at recovery of body-mass after a snow-bout, or the masses that individuals maintained under less hostile conditions.

Finally, considering the observations made with the electronic balances, numbers of birds and especially population turnover, were low in both 1991/92 and 1992/93, and the composition of the population was increasingly biased towards experienced adult males. The balances may have been more rewarding in 1988/89 or 1989/90 when turnover was high (see **5.3.4**) and fewer birds may have 'expected' supplemental food to be more or less available at all times. After six winters of supplemental food, the balances were probably sampling a fraction of the population which was far from representative of the population as a whole.

In summary, the winter ecology of this species offered a tantalising chance to study the effect of mass change on winter site choice. The results obtained were mostly consistent with the idea that snow-cover, especially in mid-winter, limits energy intake and may force some individuals, especially the young, inexperienced and female birds, to emigrate. More extensive observations of a larger and more varied selection of individuals (using a non-invasive technique such as electronic balances) are still required to consolidate these findings.

Chapter 9: SITE FIDELITY

9.1 INTRODUCTION

Chapter 5 indicated the extent to which the age and sex composition of the Cairn Gorm Snow Bunting population, and the proportion of birds which were marked, was influenced by prevailing weather conditions, but it did not describe the residency and departure patterns of individually marked birds. Fluctuations in age and sex ratios within winters could, in fact, be achieved in a number of ways, with two extremes:

i) individuals having fixed status (resident or transient) with population composition changing as a result of influxes and departures of transient individuals. This may occur in Siskins, because differences in behaviour are accompanied by, and thus may be predisposed by, differences in morphology (Senar *et al.* 1994).

ii) all individuals being transient, with differences in population composition determined by differences in the types of bird likely to visit a site at any one time. An irruptive species, such as the Evening Grosbeak, may be a good example of this strategy (Bekoff & Scott 1989, Prescott 1991).

As we have seen (**Chapter 5**), Snow Buntings seem to have an intermediate strategy. A lot more birds are caught in some winters than are seen at any one time, indicating a high number of transient birds. In contrast, some birds returned winter after winter to Cairn Gorm and obviously built up site experience. Yet others spent long periods on Cairn Gorm, but then moved briefly or permanently to other sites. The first aim of this chapter is therefore to describe the proportion of birds which become within- and between-winter residents on Cairn Gorm.

Secondly, what individual characteristics influence site establishment and fidelity? So far, I have shown that adults and males are proportionately commoner than expected at high altitude sites (**Chapter 4**), especially after differential emigration of females and juveniles following snowfalls (**5.3.5**). The results in **Chapter 6** indicated that feeding efficiency might have influenced such site use patterns, and that another attribute, namely prior experience at the site, could also increase an individual's ability to remain at a high altitude site. In **Chapter 7**, I described the pattern of dominance relationships, and suggested that winning winter interactions (referred to as dominance), although perhaps ultimately responsible for the overall differences in site use and fidelity between the sexes, may not be a good correlate of site fidelity within genders. This was because adults and experienced birds *lost* more interactions than expected, yet did not appear to suffer lower feeding efficiencies than juvenile and naive birds (**6.3**). There were also suggestions that males, adults (amongst females) and experienced individuals, but not dominants, had greater energy reserves than their counterparts (**Chapter 8**). Midwinter and high altitude body-mass peaks suggested that it was important to have large energy reserves during bad weather (**8.3.7, 8.3.11 & 8.4.2**). Site fidelity patterns amongst sex, age, experience and dominance categories could therefore help determine whether or

not the presence of such reserves could also influence the decision of whether or not to emigrate in bad weather. Furthermore, I could test whether or not site fidelity patterns were associated with having large energy reserves *per se*, by testing for differences between individuals *within* age/sex categories.

The next aims of this chapter are therefore to test whether these various attributes, predicted in earlier chapters to be of importance in establishing and maintaining site use patterns of Snow Buntings at high altitudes, help to explain the patterns of site establishment and site residency of *individually marked birds*. Unlike previous analyses, which only looked at population composition changes in relation to age/sex (**Chapters 4.3 & 5.3.5**) and whether birds were colour-ringed (a crude estimate of experience, **5.3.5**), patterns of site use of known individuals allow me to assess the roles of dominance and body-mass. It is also possible to unravel the role of site experience with more precision. Another individual characteristic which may influence site use is body-size. Ketterson & Nolan (1976) proposed that larger-bodied individuals might be more likely to survive winter at higher latitudes than smaller-bodied individuals because they have lower mass-specific metabolic rates (i.e. rate of energy use per unit body mass, Calder 1974). This increases the relative fasting endurance of large birds during severe winter storms when food is temporarily unavailable. Similar mechanisms could potentially increase the proportional representation of large birds at higher altitudes. I have already shown that large body-size does not affect dominance within genders (**7.3.3f**), so this chapter also includes tests of whether large body-size is directly associated with patterns of site establishment and residency during snow.

Finally, I attempt to look at what influences the decision to return to Cairn Gorm in further winters. This issue is complicated by the dual possibilities that birds will fail to return because they have died, or have chosen to winter elsewhere. However, individuals with high degrees of site experience might be expected to take advantage of the information which they assembled in previous winters, by returning to the site. Individuals with less site experience may be more likely to opt for other sites visited in a previous winter, or new sites. Different types of bird may benefit more from previous site experience. Therefore, after assessing and controlling for the role that experience plays in determining between-winter return rates, I test whether further differences exist between Snow Bunting age, sex and dominance categories.

9.2 METHODS

All analyses in this chapter are based on data from Cairn Gorm where the presence of colour-marked birds was recorded on a near-daily basis, and regular catches were made, throughout the winter months. Field methods and data collection are described in more detail elsewhere (**2.5, 5.2, 8.2.1**).

Firstly, a general picture of within-winter site fidelity is presented by comparing the proportion of birds of each age/sex/experience category present in Early Winter which were also seen towards the end of the same winter (in February). To remove the impact that very transient individuals would have on this result,

the analysis only included birds which were seen at least five times in Early Winter.

Next, the site fidelity of these same non-transient individuals was compared within snow-bouts. I could not do this directly, because I did not know exactly when a bird left Cairn Gorm. This transpired for two reasons. Firstly, I rarely surveyed the whole of the study area for Snow Buntings, and even if I had, I would not have seen all birds present due to their mobility and often furtive nature when feeding. This was especially true of birds feeding on natural sources at high altitudes (see **5.3.5**). However, birds were undoubtedly also missed on snowy days when the majority fed at lower altitudes (**Fig.5.4**), because they could almost always find alternative feeding sites (exposed ridges, streams, skiers' scraps and feed provided for a local Reindeer herd). Secondly, trapping, electronic weighing or behavioural observations often took precedence over inspection of flocks for marked birds. I generally tried to scan through the flock(s) and record as many individuals as possible on the first few occasions that the flock was seen each day. New individuals for the day were then added opportunistically as they were seen in the course of other observations. Inevitably, however, some birds were missed, especially when there were large numbers of marked birds present. This occurred especially in winters 1988/89 to 1990/91 when 60-80 colour-ring combinations were often recorded on a single day. Thirdly, I often provided food at two or three observation or catching sites in the same day and was not always able to spend enough time at each to be confident that I had seen all birds visiting them.

Having said all this, I hope that the birds I *did* see represented a fairly diverse cross-section of those birds present. Therefore, birds which remained on Cairn Gorm during a snow spell should have been seen more frequently during that snow spell than birds which had left (either permanently or temporarily). Moreover, the discrepancy in the number of sightings should have been greatest between residents and emigrants which left hastily and/or for extended periods. Therefore for each individual in each snow-bout, I calculated its Relative Residency during Snow. This was the proportion of days when it was seen before snow, subtracted from the proportion of days it was seen during snow-lie. Only days when some colour-ringed Snow Buntings were recorded on the Ski Area were used to calculate these proportions. I used a proportionate measure for the frequency of sightings as an acknowledgement that some birds may always have been more likely to be seen than others. Perhaps, for example, individuals differed in such characteristics as the regularity with which they visited the ski area, the number of alternative feeding locations they used in the ski area, the likelihood they would visit my bait sites, or the chance that they would be recorded if they did visit the bait (due to priority of access, trapshyness, etc.). This method was preferred to some arbitrary definition of when a bird left the ski area (e.g. not seen for three days, etc.) because it used all the data and took into account the possibility that some birds returned before the end of snow-bouts.

Relative Residency during Snow could not be compared across snow-bouts because it depended on the efficiency of resighting birds in particular snow-bouts. However, I *could* compare the Relative Residency

during Snow of individuals in the *same* snow-bout. A higher value indicated that a bird was seen relatively more often during snow than before snow, and I assumed that this was associated with greater site fidelity during the snow-bout.

Only snow-bouts where the first day of snow was in Early/Mid Winter were used. Non-transients were selected by only including birds if they were seen in both the present and previous snow-bouts. Birds caught in a particular snow-bout were excluded to eliminate the possibility that birds moved away because they were trapped. The Relative Residency during Snow of gender, age and experience categories of birds was compared using Mann Whitney U-tests, whilst the effects of dominance and body-size (as estimated by wing-length) were tested using Spearman Rank correlations. Overall trends were examined by grouping the separate tests for each snow-bout using Combined Probability Tests.

The probability that new birds visiting the site would become established as residents was investigated by looking at whether birds trapped for the first time were subsequently resighted. Resightings were grouped into four time intervals, i.e. 1-2, 3-7, 8-30 and 31+ (but same winter/spring) days after first capture, and an individual was simply recorded as being seen or not seen during each of these periods. As birds seen in one of these periods also tended to be seen in other periods (see **9.3.3**), I selected the period 8-30 days post-capture to look at factors affecting the fidelity of these newly trapped birds. Over a shorter period birds may not have experienced conditions liable to cause them to move site, while the longer (31+ days) period was avoided because birds caught late in the winter would have had less chance of being resighted prior to migration than early winter birds. Breeding birds were omitted from these analyses because they may have been more likely than winter immigrants to leave the site then come back within 30 days.

The percentage of birds resighted 8-30 days post-capture was compared to weather conditions on and after 45 winter catch days when at least five new birds were captured. Five weather variables were used (9AM & MEAN TEMPERATURE, WIND SPEED, SNOW COVER and DEPTH) and four predictor variables were derived from each of them: the value of the weather variable on the catch day, the value on the next day, the mean of the values on the catch and the next day, and the mean value during the next week (including the catch day). SNOW DEPTH was categorised prior to calculating these variables as 0=no snow, 1=1-9cm of snow, and 2=10+cm of snow. The percentage of birds resighted was then regressed on the values of each of the predictor weather variables.

The influence of age/sex category and body-mass on the proportion of birds which were resighted 8-30 days post-capture was investigated using loglinear tests. Age/sex was entered as one variable with four categories in these tests to reduce the potential for higher order interactions. Body-mass was entered as residual mass. This was categorised as being 1g or more below the expected mass of the individual (as calculated using the parameters given in **Table 8.1**, except for the time correction which was seasonally adjusted, based on the formula in **Table 8.3**), within 1g of the expected mass, or 1g or more above the

expected mass. These categories formed 38%, 34% and 28%, respectively, of the 566 body-masses from newly trapped individuals. As an alternative method, lest bias existed in the age/sex and/or mass composition of catches, I also divided each catch into three equal parts based on residual mass (two catches with only two individuals were omitted). Thus a catch specific mass (lightest third, middle third or heaviest third of the catch) was entered into the loglinear model instead of residual mass.

Finally, I present data on between-winter return rates to Cairn Gorm, using a combination of chi-square and loglinear tests. I test for differences between breeders and winter immigrants, between years, between age, sex and dominance categories of winter immigrants, and in relation to site experience (in terms of how many times a bird was seen in the previous winter, and how many previous winters a bird had been seen).

9.3 RESULTS

9.3.1 Within-winter site fidelity

A rough overall indication of site fidelity of established wintering birds was given by the percentage of birds seen in Early Winter which were still present in late winter. Altogether, 80% of Snow Buntings seen at least five times on Cairn Gorm in November or December were also seen in February (i.e. towards the end of the winter), and this percentage did not vary significantly between years (X^2_4=4.24, P>0.3). A loglinear model indicated, however, significant and independent effects of sex and status (juveniles, naive adults and experienced adults, as defined in **6.3.2b**) on the percentage of birds resighted in February. Males were more likely to be seen in February than females, and experienced adults were more often still present then than inexperienced adults, whilst inexperienced juveniles were intermediate (**Fig.9.1**; loglinear model, significance of interactions between: resighting and sex, X^2_1=4.41, P=0.036; resighting and status, X^2_2=8.77, P=0.012; higher order interaction, X^2_2=2.02, P=0.36).

9.3.2 Site fidelity within a snow-bout.

Were particular categories of Snow Buntings more likely to stay at Cairn Gorm during snowfalls than others, and if so, was this relationship affected by characteristics of the snowfall such as snow depth, duration or timing? This was investigated using the 23 occasions during winters 1988/89 to 1992/93 in which observations of colour-ringed birds were made both before and during a spell of snow-lie. In three cases the effect of age, and in two cases the effect of experience, could not be tested within a snow-bout because there were no juveniles or inexperienced birds present, respectively, to meet the conditions of the tests (see **9.2**). Similarly, the effect of dominance was not tested in one snow-bout because only three birds were of known win proportion when adult (see **7.3.3d**).

Combining all relevant Mann-Whitney U-tests or Spearman Rank correlations, neither age, sex, experience,

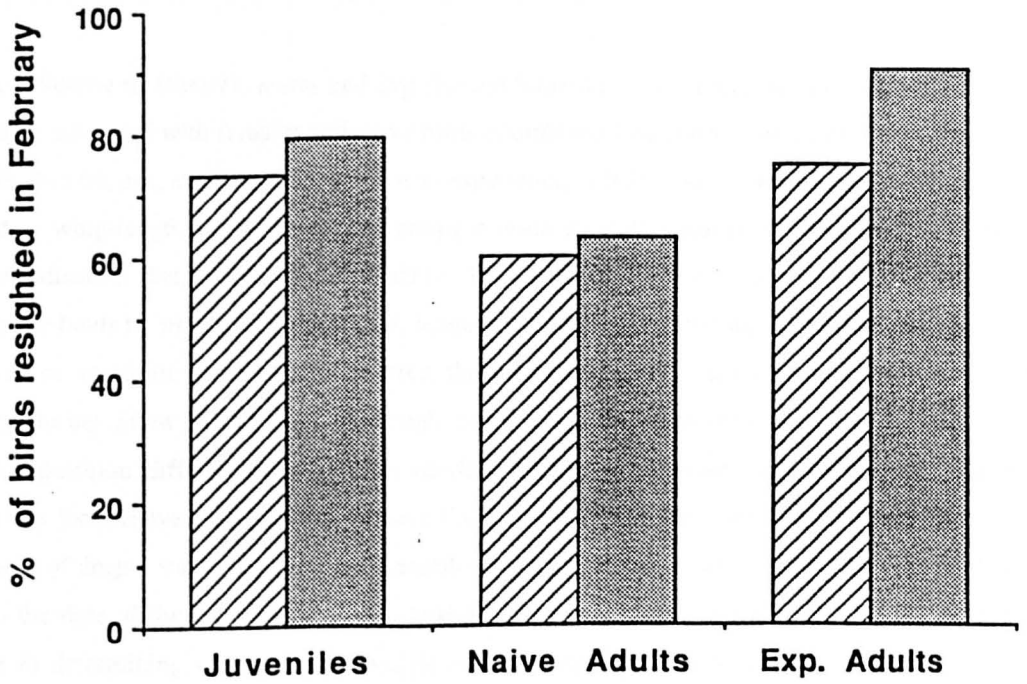


Fig.9.1. The percentage of Snow Buntings seen at least five times in Early Winter which were resighted in the next February in relation to their sex and status. *Hatched bars represent females, stippled bars males. Sample sizes (left to right) are 15, 19, 25, 19, 48 & 116 birds. Males, especially those with previous site experience, were more likely to be still present in February (see text for statistics).*

size or dominance affected a bird's Relative Residency during Snow (Combined Probability Tests: sex, sum of lnP=-17.5, n=23 tests, n.s.; age, sum lnP=-7.7, n=20, n.s.; experience, sum lnP=-27.6, n=21, P<0.1; size, sum lnP=-14.5, n=23, n.s.; dominance, sum lnP=-0.65, n=22, n.s.). Considering all 20-23 Mann-Whitney U-tests separately, Relative Residency during Snow was significantly higher for males than females on five occasions (but vice-versa on two), significantly higher for adults than juveniles twice, and significantly higher for experienced versus inexperienced birds on four occasions. Interestingly, both tests indicating that females had higher Relative Residency during Snow than males were in 1991/92 and 1992/93, whilst in none of the eleven snow-bouts during these winters were males, adults or experienced birds shown to have higher Relative Residency during Snow than their counterparts. These winters, however, were unusual because they had much lower turnover rates of Snow Buntings than in other winters (see **Table 5.4**). The rest of this section therefore only considers snow-bouts during the three winters 1988/89 to 1990/91.

In winters 1988/89 to 1990/91, males and experienced birds were seen relatively more often during than before snow compared with females and naive birds (Combined Probability Tests: sex, sum of lnP=-19.6, n=12 tests, P<0.05; age, sum lnP=-7.5, n=10, n.s.; experience, sum lnP=-23.6, n=11, P<0.01). Body-size, as estimated by wing-length, did not produce a stronger result than sex (sum lnP=-16.1, n=12, n.s.) nor was there any indication that, within gender, Relative Residency during Snow was affected by size. I then divided snow-bouts by time within the winter, length of snow-lie, and maximum depth of snow to find out whether these variables differentially affected the influence of sex, age or experience on Relative Residency during Snow (**Table 9.1**). Although using these crude techniques it was not possible to completely partition differences in relative residency amongst different potential causes, **Table 9.1** indicates that females were more likely to leave Cairn Gorm during snow spells later in the winter, or in longer spells of deeper snow (the latter two variables were correlated - r_S=0.73, P=0.008 - but neither was related to the date of the first day of snow - both P>0.6). Age, on the other hand, may be particularly important in determining whether an individual stays through an early season snow-bout. Greater site experience appeared to increase the probability of staying at all times and under most conditions.

In only one snow-bout (in 1992/93) was Relative Residency during Snow significantly related to dominance, and in this case the result was the opposite of what might have been expected: dominant birds were seen relatively less often during than before snow compared to subordinates. There was no suggestion that dominants were more likely than subordinates to have higher Relative Residency during Snow in 1988/89 to 1990/91 (Combined Probability Test, sum of lnP=-5.40, n=11, n.s.), nor in early/late, prolonged or heavy snow-bouts.

Table 9.1. Results of Combined Probability Tests on the effect of sex, age and experience on Relative Residency during Snow in different categories of snow-bout.

	Sex:			Age:			Experience:		
	Sum lnP	n tests	P	Sum lnP	n tests	P	Sum lnP	n tests	P
First day of snow in:									
November/December	0.5	4		-7.1	2	**	-7.5	3	*
January/February	-20.1	8	***	-0.4	8		-16.1	8	**
Length of snow-lie:									
1-4 days	-6.0	4		-1.1	4		-10.4	4	**
7-40 days	-13.5	8	*	-6.4	6		-13.2	7	*
Maximum depth of snow:									
2-10cm	-2.1	5		-5.8	4		-12.1	4	**
12-43cm	-17.5	7	**	-1.6	6		-11.5	7	

*** P<0.001, ** P<0.01, * P<0.05

9.3.3 Determinants of residency of newly arrived birds

This section, in contrast to the previous two sections which looked at patterns of site fidelity in Snow Buntings which had become established on Cairn Gorm, describes the rate at which newly arrived Snow Buntings became established at the site. It also looks for variation in the establishment rate associated with the weather conditions which prevailed at and just after the time of capture, and for differences between individuals.

Altogether, 32% of 591 newly caught birds on Cairn Gorm were resighted within two days of first capture, 52% within the first week, 60% within 30 days and 63% at some stage during the same winter. Some 40% were resighted in the period 3-7 days post-capture, 42% 8-30 days post-capture, and 34% thereafter. However, 53% of birds were not seen again more than a week after first capture. Although all birds seen during a later period had not necessarily been seen in all earlier periods, the probability of being sighted in

a later period was significantly greater if the bird had also been seen in an earlier period (**Table 9.2**). Thus if resightings in a chosen period were taken to indicate site residency, the categorisation of an individual as resident or itinerant would in many cases be the same whichever resighting period was chosen. However, for reasons outlined in **9.2**, I consider individuals resighted in the period 8-30 days post-capture as having become established on Cairn Gorm.

The percentage of birds resighted 8-30 days after a catch was significantly correlated with only one of the 20 predictor weather variables (**Table 9.3**). More birds were seen again if the 9AM TEMPERATURE on the catch day was low. This was opposite to what was expected, because residency was predicted to be higher if intervening conditions were less harsh. As residency is more likely to depend on longer term trends in weather (such as the 8-day averages), and these were not significantly related to the percentage of birds retrapped, I conclude that, although the probability of becoming resident may be related to weather in the intervening interval, the relationship cannot be simple and may be obscured by interactions between the variables and other possible explanatory variables (population size, time of year, etc.).

Table 9.2. The percentage of newly-trapped individuals which were resighted in a given interval post-capture (p-c), in relation to whether or not they had been resighted in a previous post-capture interval.

		% (n) resighted in second interval if:			
First interval	Second Interval	not seen in first	also seen in first	X^2_1	P
1-2 days p-c	3-7 days p-c	28 (399)	65 (191)	70.5	***
	8-30 days p-c	36 (399)	56 (191)	20.7	***
	31+ days p-c	29 (399)	44 (191)	13.1	***
3-7 days p-c	8-30 days p-c	21 (353)	74 (238)	159.5	***
	31+ days p-c	20 (353)	55 (238)	76.7	***
8-30 days p-c	31+ days p-c	8 (340)	69 (251)	240.0	***

*** P<0.001

Table 9.3. Spearman Rank correlations between the percentage of birds resighted 8-30 days post-capture, and various weather variables on and after the day of capture. *The value of a variable for 'Both Days' was the mean of its value on the catch and the next day, whilst the value over the 'Whole Week' is the mean of the eight readings on the catch day and over the next week. n=45, except for 9AM TEMPERATURE which was not measured in 1988/89, hence n=34.*

	Catch Day		Next Day		Both Days		Whole Week	
	rs	P	rs	P	rs	P	rs	P
WIND SPEED	-0.09	0.54	-0.03	0.84	-0.08	0.61	-0.06	0.71
SNOW DEPTH	0.24	0.11	0.13	0.39	0.18	0.23	-0.16	0.29
SNOW COVER	0.09	0.56	-0.08	0.61	-0.02	0.89	-0.18	0.23
MEAN TEMPERATURE	-0.23	0.14	-0.03	0.83	-0.12	0.43	0.04	0.79
9AM TEMPERATURE	-0.36	0.04	-0.20	0.26	-0.30	0.09	-0.22	0.21

Next, I examine individual influences on the probability of becoming established. Both age/sex category and residual body-mass had strong and independent effects on the probability of being resighted 8-30 days post-capture (**Fig.9.2**; loglinear model, significance of interactions between: resighting and age/sex, X^2_3=36.3, P<0.001; resighting and residual mass, X^2_2=26.8, P<0.001; higher order interaction, X^2_6=1.92, P=0.93). Birds were more likely to be resighted if they were heavy when first captured, and if they were male. The results were similar when relative mass within a catch was used instead of overall residual mass. Gender, rather than size *per se*, again appeared to induce the difference between the sexes: within sex and mass groupings, birds which became established were not consistently larger than those which did not (oneway ANOVAS on wing-length: minimum P value > 0.3).

9.3.4 Return rates between winters

Two eventualities will reduce the number of migrants which return to a wintering site year after year, namely death and emigration. These are usually difficult to separate in practise, unless data is also available from the breeding grounds. This section describes the pattern of between-winter returns of Snow Buntings to Cairn Gorm, and examines some factors which may have influenced losses of birds, either through mortality or emigration.

Firstly, were local breeders more likely to return than winter immigrants? Within the wintering flock there were always some local breeding birds which had travelled only 0-12km to reach the Cairn Gorm Ski Area.

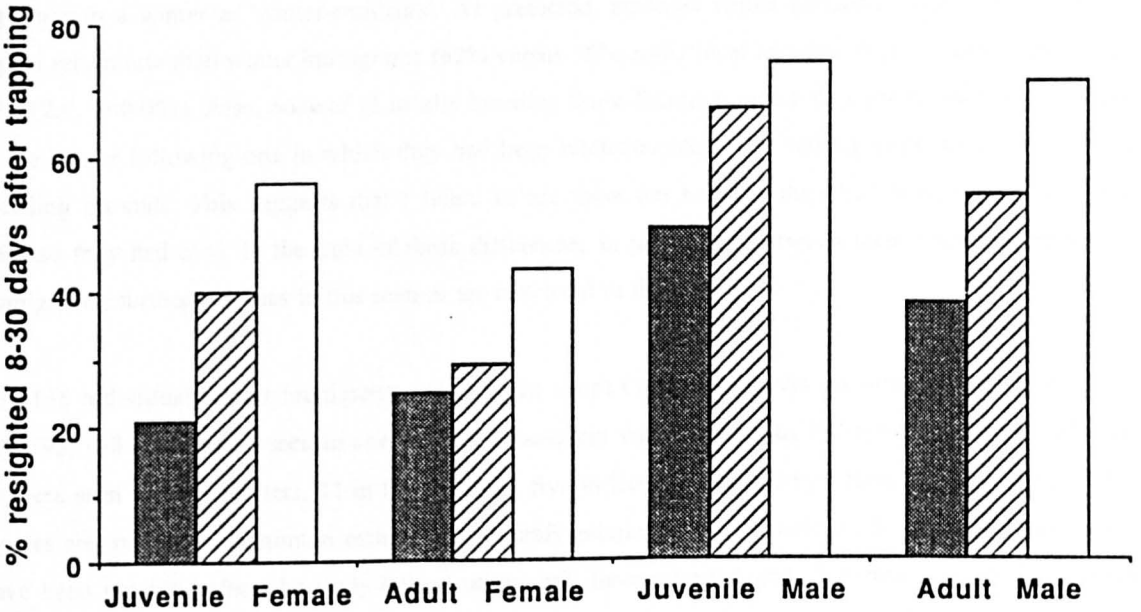


Fig.9.2. The effect of age/sex category and mass when captured on whether or not individual Snow Buntings were resighted on Cairn Gorm 8-30 days post-capture. *Stippled bars represent birds which were 1g or more under expected mass (for the day, time, sex and size of the bird), hatched bars represent birds within 1g of the expected mass, and blank bars represent birds 1g or more over the expected mass. Sample sizes (left to right) are 47, 43, 18, 69, 78, 76, 43, 30, 35, 58, 41 & 28 birds. Resighting rates were higher if the individual was heavy and/or male.*

Because site experience was expected to have allowed them to survive more easily on Cairn Gorm in subsequent winters, and site quality is probably relatively high at this site (see 4.4), I would have expected few local breeders which had become established on Cairn Gorm in a given winter to move further away in subsequent winters. On the other hand, winter immigrant Snow Buntings could choose to try to winter at better sites further north. If mortality rates of breeders and winter immigrants were equal, I would expect the between-year return rates of breeders to be no less than, and possibly more than, those of winter immigrants.

Comparison of return rates between winters could have been confused, however, by differences in the proportion of birds which were 'transient' at Cairn Gorm each winter. I therefore defined birds with 10+ sightings in a winter as 'winter-residents'. As predicted, amongst winter-residents, local breeders had a higher return rate than winter immigrants (62% versus 35%, n=53 local breeders & 364 winter immigrants, $X^2_1=12.9$, $P<0.001$). Also, none of 11 locally breeding Snow Buntings which failed to return to Cairn Gorm in the winter following one in which they had been winter-resident was subsequently seen again on the breeding grounds. This suggests that I failed to see them not because they had moved elsewhere, but because they had died. In the light of these differences in return rate between local breeders and winter immigrants, further analyses in this section are restricted to the latter.

Of 1138 individual winter immigrants captured on Cairn Gorm during the six winters from 1987/88 to 1992/93, 168 (15%) were seen in one or more subsequent winters. In total, 115 were seen in two winters, 35 were seen in three winters, 11 in four winters, five in five winters and two birds in six winters. These figures are, of course, minimum estimates of overall return rates to Cairn Gorm because some birds will have been present before the study began, others will have returned after it ended, and some were not individually marked in 1987/88. For this latter reason I have only used data from 1988/89 onwards during further analyses.

There were 216 returns (involving 146 individual winter immigrants) during the period 1988/89 to 1993/94. 94% of these occurred in the winter immediately following the last winter in which the individual was seen, but in nine cases (three males, six females) a bird was not seen in one intervening winter, one female was 'missing' for two winters, and two females were missing for three consecutive winters.

To examine for annual variation in return rates, I again chose to reduce the influence of transient individuals by comparing the return rates between winters of birds which were present in the first winter on at least ten occasions (winter-residents). No significant difference in annual return rate was detected (range 27-45% returning between winters, n=39-113 birds each winter, $X^2_4=8.51$, $P=0.07$). Therefore data for all years were combined.

If site information was a valuable asset, I would predict that birds which had more information, as

estimated by the number of times they were seen to be present, would be more likely to return to the site in future winters. I firstly examined this in naive individuals, i.e. they were caught for the first time in the winter under consideration. As expected, the more often a naive winter immigrant was seen within one winter, the more likely it was to be seen in the next (**Fig.9.3**; $X^2_4=112.2$, $P<0.001$). Interestingly, the return rates of *experienced* birds showed a similar pattern (**Fig.9.3**; $X^2_4=15.1$, $P=0.005$). In experienced birds, lower return rates of individuals with low numbers of sightings (compared to those with more sightings) may be a result of within-winter mortality, or establishment at an alternative site in the same winter.

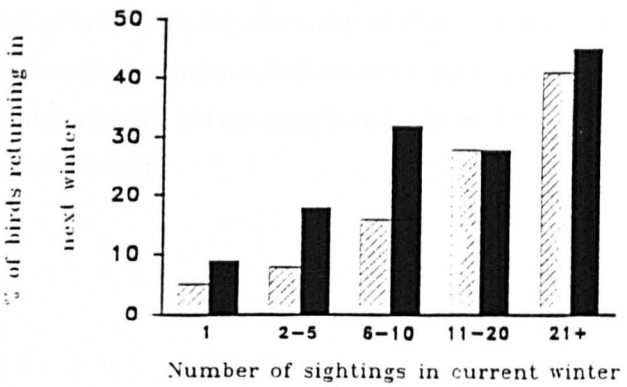
Examination of **Fig.9.3** seemed to suggest, however, that return rates of experienced versus naive birds were higher if the individual was only seen on a few occasions (three left-hand pairs of bars), but that returns were independent of experience if an individual was seen on over ten occasions (two right-hand pairs of bars). I confirmed this using loglinear models which retained the influence of the number of sightings on return rates. Overall, experienced birds with fewer than ten sightings were more likely to return than naive birds with fewer than ten sightings (significance of return*experience term, $X^2_1=6.06$, $P=0.014$), but the likelihood that a bird would return did not depend on experience if the individual was seen 11-20 or 21+ times ($X^2_1=0.13$, $P=0.72$). Moreover, it appeared that returning in one winter did not affect the chances of returning in a future winter (**Fig.9.4**).

Another factor which could affect the probability of returning in the next winter was whether or not an individual was seen towards the end of the current winter. Lack of sightings could indicate emigration or mortality. In support of this, no bird seen more than ten times in a winter yet not in February or later, returned in the next winter. This was significantly different from the number expected to return if presence in late winter/spring was not an important determinant of return rates ($X^2_1=10.7$, $P=0.001$). Because I was mainly interested in how individual attributes affected the likelihood of returning to Cairn Gorm between the *end* of one winter and the start of the next (within-winter variation in emigration/loss having been reported in the previous sections), I also included presence in February or later as a condition for inclusion in the final group of analyses.

To assess the relative return rates of each of the sex/age/experience categories of long-established winter immigrant Snow Buntings which had probably survived the winter, I selected those individuals which had been seen at least 20 times in the current winter up to at least February. Return rates in this group were higher in males than females (50% versus 29%), but did not vary significantly between the age/experience categories (**Fig.9.5**; loglinear model, significance of return*sex term, $X^2_1=7.23$, $P=0.007$; return*status, $X^2_2=1.96$, $P=0.38$; higher order interaction, $X^2_2=2.14$, $P=0.34$).

Return rate was not related to dominance (ANOVA on win proportion when adult, comparing birds which returned and those which did not: $F_{1,159}=0.78$, $P=0.38$; a similar result was obtained if the analysis was confined to the 124 males, or the 77 adult males). To see if the difference in competitive ability between

Fig.9.3. The relationship between return rate and the number of winter sightings for naive (hatched bars) and experienced Snow Buntings (filled bars). *Sample sizes are (left to right) 403, 22, 310, 22, 115, 28, 96, 47, 85 & 112 birds. Return rates were higher for birds seen more frequently, and, for birds with few sightings (up to ten), were greater in experienced individuals (see text for statistics).*



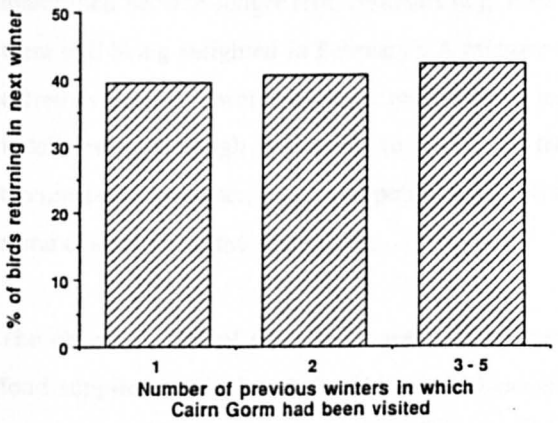
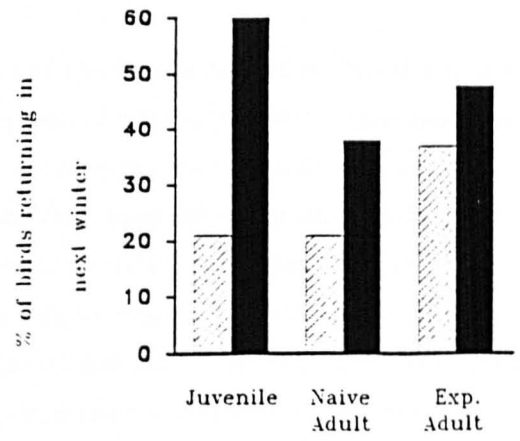


Fig.9.4. The percentage of winter immigrants which returned to Cairn Gorm in the next winter (x+1) in relation to the number of winters they had already returned to Cairn Gorm. *Only birds which were seen at least ten times in winter x were included. Sample sizes (left to right) were 109, 37 & 19 birds. There was no difference in the tendency to return as the number of previous returns increased ($X^2_2=0.05$, $P=0.97$).*

Fig.9.5. The return rate to Cairn Gorm of long-established (more than 20 sightings in the current winter) Snow Buntings in relation to sex and status. *Females are represented by hatched bars, males by filled bars. Local breeding birds and birds not seen in or after February were omitted from the analysis. Sample sizes (left to right) are 14, 37, 14, 16, 30 & 81 birds. Males were more likely to return than females, but no effect of status could be detected.*



adult and juvenile males could be partially attributed to variation in the return rate of juvenile males (see **7.3.3c & 7.4.4**), I compared the WPAs of juvenile males which returned with those which did not. Juvenile males which were not resighted in the next winter had marginally, but not significantly higher WPAs than those which were resighted (0.56 versus 0.51, $F_{1,32}$=0.39, P=0.54).

9.4 DISCUSSION

9.4.1 Within-winter site fidelity

Clearly two extreme types of Snow Buntings visited Cairn Gorm. First, over 50% of newly trapped birds were not seen again more than a week after capture; these transient birds may have been unable or unwilling to become established on Cairn Gorm, and may have died, adopted a continuously transient lifestyle, or became resident elsewhere. Second, of the birds which stayed on Cairn Gorm for a short time, many then became longer term residents (e.g. 80% of the birds with five or more sightings in Early Winter were still being resighted in February). A mixture of degrees of site fidelity were observed between these extremes: residents were not career residents, i.e. having become established, they did not remain at the site indefinitely. Although impossible to prove, the fate of newly arrived birds may also have depended on circumstance (weather, mass, competitors, etc.): it is possible that all birds would have become resident, to some extent, given the opportunity.

The observed rates of site fidelity were almost certainly inflated, possibly to a large extent, by artificial food supplies available on the Ski Area (skiers discards, reseeded areas, etc. but especially my baited areas). Hopefully, however, the same factors which encourage greater degrees of site fidelity under these artificial conditions, i.e. sex, age, experience and body-mass, would also be pertinent in natural situations. Perhaps dominance would have a greater influence on site fidelity if birds had to resort to small, patchy natural food resources, but it can also be argued that the importance of age, site experience and mass reserves may also be heightened in such circumstances, resulting in larger changes in population composition than observed in this study.

Sex was an important determinant of whether or not a bird became established on Cairn Gorm, and, having become established, whether or not it stayed during bouts of bad weather. Males were more likely to do both. Perhaps this was because males were larger. But body-size, as estimated by wing-length, did not explain additional variation in site fidelity patterns. This counteracts the possibility that mass-specific metabolic rate, which is lower in larger birds therefore increasing their relative ability to fast for long periods, affects site fidelity during snowstorms. This may be because birds may still be able to feed under almost any weather conditions, albeit it at a reduced and sometimes insufficient rate. Under such circumstances, the small amounts of food eaten may come closer to meeting the lower energy requirements of smaller birds, thus reducing the disadvantages of having lower mass-specific metabolic rates. Such an

argument also negates the suggestion that body-size differences between the sexes influence differential migration patterns because of variation in mass-specific metabolism (The Body-Size Hypothesis - Ketterson & Nolan 1976). Mass-specific metabolic rate would only be influential in such circumstances if feeding was almost impossible for long periods. Furthermore, if small amounts of food *were* available, favouring small birds, dominance advantages associated with being larger could again reverse any size-specific metabolic advantage.

Sex and rank have been inferred as correlates of site fidelity elsewhere (Balph 1979, Rabenold & Rabenold 1985, Terrill 1987, Pattenden & Boag 1989, Senar *et al.* 1992a), but in most cases the effect of gender has usually been assumed to be due to, or compounded by, a difference in competitive abilities between the sexes. Here greater residency of males during snow occurred in the absence of any clear dominance advantage enjoyed by birds with high relative resighting rates during snow. Therefore the difference between sexes was probably independent of direct male dominance over females. Females may simply have evolved to leave a deteriorating site at an earlier stage than males, irrespective of their phenotypic competitive abilities.

Having become established, experience at the site may override sex-specific dominance as the most important factor controlling future residency. However, sex-specific characteristics may still act on females to make them leave the site earlier, particularly when conditions become particularly severe. At such times, birds may be forced to use smaller food patches in larger, denser flocks, a situation which reduces the feeding efficiency of females in relation to males. Females had particularly low relative resighting rates when the snowfalls were deep or prolonged, or late in the winter when, due to presumably dwindling seed stocks, food was probably more difficult to obtain.

In contrast to the lack of a direct influence of dominance on resighting rates during snow of established birds, it is possible that phenotypic traits, including a bird's relative aggressiveness and willingness to compete, as well as its agonistic ability, could influence a newly-arrived individual's decision of whether or not to stay at a site. The relative dominance of naive over experienced Snow Buntings (**7.3.3a**) indicates that individuals may have been more aggressive when they first arrived than after they had become established. Unfortunately, it was impossible to look for differences in aggressiveness (as measured perhaps by initiation or escalation rates) between birds which did or did not become established, or for changes in aggressiveness with time after establishment, because of the small sample of encounters which involved inexperienced individuals within a few days of their arrival. Future studies could, however, address these problems by targeting their observations on such birds.

The effect of age on site fidelity in birds with no previous site experience was perhaps opposite to that expected. Having been seen at least five times in Early Winter, naive adults were not seen more often than juveniles in February (**Fig.9.1**), and newly-trapped adults tended to have lower rates of becoming

established than newly-trapped juveniles (**Fig.9.2**). Although neither of these results reached significance, this outcome might, in fact, have been expected if naive adults were more likely to be established at sites nearby. Juveniles, of course, will not have had experience at other sites in previous winters. Moreover, if a proportion of birds were 'career transients' while others were 'potential settlers', then a higher proportion of juveniles which were 'potential settlers' may have stayed because many of the adults in this category would already have settled in earlier winters.

In birds which had become established on Cairn Gorm, age was only important in determining the Relative Residency during Snow in snow-bouts in Early Winter. At this point the learning curve may still have been steep for juveniles, and they may not be willing to take the risk of remaining at high altitudes during bad weather until later in the winter. Previous site experience, however, was the best overall predictor of whether or not an individual was seen more often than expected during snow, significant differences being observed even during moderate or brief snowfalls. Basic information on whether and where food will appear during snowfalls, and perhaps the knowledge that it has already competed successfully for food during previous spells, are therefore probably influential in a bird's decision of whether or not to remain at a site during bad weather.

Neither age, sex nor experience influenced the Relative Residency during Snow of long-established Snow Buntings during 1991/92 or 1992/93. Both winters were characterised by low numbers and turnover of birds (**Table 5.4**), which may have reduced competition and enabled birds to assimilate site knowledge more rapidly without ever experiencing great hardship. Therefore more vulnerable individuals, such as females, juveniles and birds with less previous site experience, may not have been forced to abandon the site due to lack of food or the threat of future low intake rates.

Several authors have implied that mass loss, or the risk of mass loss and ensuing starvation, may influence whether a bird becomes resident in an area or moves on (e.g. Lundberg 1985, Terrill 1987 & cited references). I am aware, however, of only one previous study of wintering birds which has shown a difference in mass between individuals which became resident and those which were transient. Senar *et al.* (1992a) showed that Siskins which were resident at a site where excess food was provided, were heavier than transient individuals. This difference was evident even on the first day that future residents arrived. As with Snow Buntings, it was not possible to decide whether birds became residents because they were heavier (as a result of social dominance in Siskins), or because it was advantageous for transient individuals to remain light because travel costs between sites were higher. In the case of Siskins, the latter explanation may be more plausible because differences in residency status are also associated with differences in wing shape (Senar *et al.* 1994). In theory, birds with less predictable food supplies (presumably transients) should try to *increase* their energy reserves (Houston & McNamara 1993). I therefore favour a direct explanation for the greater body-mass of Snow Buntings which became established compared to those which did not: they could risk staying on Cairn Gorm in worse conditions than their counterparts without

incurring the same starvation risk, thus gaining invaluable site experience. Once established, the relationship could work in reverse: experienced birds were heavier than inexperienced birds prior to snow and may be more able to maintain positive energy budgets (see **8.4.4**).

9.4.2 Between-winters site fidelity

In many migratory species individuals have been shown to return year after year to the same non-breeding sites (see review by Gauthreaux 1982, also Metcalfe & Furness 1985, Townshend 1985, Diefenbach *et al.* 1990, Piper & Wiley 1990a, Nolan & Ketterson 1991, Percival 1991), although some individuals may move long distances to other wintering areas (e.g. Spaans 1977). Previous knowledge of a site will obviously improve an individual's chances of survival if conditions and resources at the site are related between winters, thus favouring site fidelity.

In this study it was rare for a Snow Bunting to be absent from Cairn Gorm in a winter yet be present in both the preceding and following winters. This suggests that movements to new sites or areas, perhaps further north (see **5.3.6**), were largely permanent. The advantages of residency at a site, once established, may overcome any benefits of not exploring new wintering areas, and may also be greater than those of trying to become established in a superior habitat elsewhere. However, costs of ignorance, particularly for females when bad conditions force them to emigrate temporarily, may also be high, and favour at least occasional sorties elsewhere.

Local breeding Snow Buntings, known to be alive from breeding observations (Smith & Marquiss in press a), did not 'skip' any winters on Cairn Gorm once they had become established there. Such birds were wintering as near as possible to the breeding grounds, and, if high altitude habitat is the best habitat available to Snow Buntings (see **4.4**), they could not move to better quality habitat. Local breeders that wintered on Cairn Gorm also had higher annual survival rates than local breeders that were not seen in winter (71% versus 44%, unpubl. data), indicating the benefits of wintering at high altitudes (although variation in bird quality and/or artificial feeding may also have been partly responsible).

Altogether, 50% of winter immigrant males which were long-term residents on Cairn Gorm, and were still present in or after February, returned to Cairn Gorm in the next winter (**Fig.9.5**). These may be equivalent in quality to the migrant section of the Scottish breeding population (since they have departed from breeding grounds in Iceland or beyond). Their return rate therefore compares favourably with the survival rate of Scottish migrant breeders (44%). However, the return rate of winter immigrant males is not an annual rate: by definition they 'returned' even if only seen once in November of the returning year. Even if all males which survived also returned to Cairn Gorm (rather than wintered elsewhere), annual survival would be 50% *minus* mortality between November/December and February. On average, 50-60% of male Snow Buntings on the Arctic breeding grounds are adult (more than one year old; Meltofte 1983), which,

for a constant population size would indicate that annual survival rates are in the region of 50-60%. Even if the males which came to Scotland were of slightly poorer quality than males which wintered nearer their breeding grounds, and therefore had a slightly lower survival rate, it could still be possible that a small percentage of long-established immigrant males at Cairn Gorm disappear between winters because they have *chosen* to winter elsewhere, rather than died (see **5.3.6** & Banks *et al.* 1991b for apparent examples of this).

The composition of some Snow Bunting breeding populations is apparently biased towards males (reviewed by Meltofte 1983), but this may be due to the greater difficulties of counting breeding hens than singing males (Watson & Smith 1991). In Scotland, sex ratios of breeding birds are close to unity, and no difference between genders has been noted in the resighting rate of marked birds between summers (Smith 1994 and further unpubl. data). The much greater tendency for long-established immigrant males, compared with females, to return to Cairn Gorm (50% versus 29%, **Fig.9.5**), is therefore unlikely to be solely due to differences in survival between genders. The difference in return rates between sexes is consistent with the greater tendency for females to move away from Cairn Gorm soon after arriving there (**9.3.3**), and their greater tendency to move away during bad weather (**9.3.2**). Attachment to a site may simply not be so well-developed in females because they are unlikely to compete successfully with males. As they are more likely to be forced to move away from a site in extreme weather, it would be more advantageous for females than males to have some knowledge of alternative venues (see Evans 1981 and Diefenbach *et al.* 1988 for examples of how predictability of access to food might select for nomadic versus sedentary behaviour).

Only Piper & Wiley (1990b) have reported between-winter return rates of migrant passerines in relation to dominance. High ranking White-throated Sparrows were more likely to be seen in subsequent winters than subordinate birds, but this was attributed to differential mortality, rather than to a difference in fidelity to a site. In my study there was no difference in return rates in relation to rank (apart from a clear tendency for females to be less site faithful), suggesting similar mortality and fidelity rates in birds of different rank. Alternatively, of course, dominants (or subordinates) might have higher survival rates *and* be more likely to winter further north in subsequent winters (survival gains therefore balancing emigration losses), but there is no evidence for either.

Interestingly, beyond a certain level of site experience within a winter (10-20 sightings), age and prior site residence (years) made little difference to the probability that birds would return in future years (**Figs.9.4 & 9.5**). Additionally, having returned once, a bird was not even more likely to return again (**Fig.9.4**). This may be because the extra site information accrued on each day present on the site rapidly levels off over a period of weeks or months. Juveniles and naive adults, having survived through several spells of snow, will get to know where and when to expect food in future, and having been able to survive through a few bouts of bad weather, may be as able to survive other snow-bouts as experienced adults. In support of this, age

was only an important indicator of relative residency during snow early in the season. Previous site experience always improved relative residency during snow, but there were almost always some naive individuals attempting to settle on Cairn Gorm during the winter. However, the relative contribution to the significance of the Combined Probability Test for experience of the three Mann-Whitney U-tests in Early Winter was slightly greater than the eight tests in Late Winter (mean sum of lnP=2.5 versus 2.0). This suggests that the presence of 'experienced' inexperienced individuals may have watered down the influence of 'new' inexperienced individuals later in the winter. Having survived at a high altitude site for a given period (20 sightings were equivalent to at least 6 weeks residency on Cairn Gorm), random factors affecting survival and emigration may have obscured any continuing influence of site experience on residency.

Chapter 10: CONCLUSIONS AND SPECULATIONS: AN OVERVIEW

10.1 Itinerancy in relation to winter distribution and weather patterns

As expected from previous observations of wintering Snow Bunting populations (Dementiev & Gladkov 1954, Nethersole-Thompson 1966, Lambert 1986, Banks *et al.* 1991b), numbers fluctuated widely on Cairn Gorm over the course of a winter. Because they increased at times, as well as decreased, this was indicative of population movements rather than mortality. Prys-Jones (1984) discusses the winter distributions of a guild of small, north-temperate passerines (mainly buntings, sparrows, fringilline finches and larks) which frequently feed on the ground. Many avoid wintering in regions with deep snow-cover or low temperatures, whilst others, notably the House Sparrow, may only survive in such areas as a result of human activities. However, Snow Buntings, it was suggested, survived as a result of "a capacity for extremely high mobility between unpredictably available areas of food". It was therefore no surprise to find that, in common with other British ground-feeding open-country species (e.g. grazing wildfowl species, Red Grouse, Ptarmigan, Lapwing, Golden Plover, Snipe, Skylark, Meadow Pipit, Fieldfare, Song Thrush, Redwing, Greenfinch, Linnet - see various authors in Lack 1986), changes in Snow Bunting distribution patterns were mainly associated with snowfalls. However, as with the other two species found mainly in upland regions where snowfalls will be most frequent (Red Grouse and Ptarmigan), Snow Buntings seem well capable of coping with snowy conditions and showed mostly local (20-50km) movements within winter periods, rather than long cold-weather movements to the south and west of Britain or beyond.

10.2 Weather and behaviour patterns

Although I could make few behavioural observations of flocks in natural situations, it is likely that the changes in behaviour and energy reserves seen following snowfalls at the semi-natural study site were similar to those occurring naturally, although probably somewhat modified. Snowfalls may have reduced both the area of high ground suitable for feeding on Cairn Gorm (**5.3.4**), and the size and abundance of available food patches on lower ground (flushes, wind swept areas or areas where seed heads of longer-stemmed hill grasses protruded through the snow). During the deepest snowfalls, most birds probably departed, or at least would have done if I had not provided supplemental feeding opportunities. Snowfalls therefore appeared to concentrate Snow Buntings around good feeding patches, increasing densities and hence leading to an increased rate of interaction between birds (**7.3.1b**). There was also evidence that snow or cold temperatures themselves tended to make birds squabble more frequently, independently of changes in flock-size (**Table 7.2**), and possibly even cause some birds to defend good feeding patches (**7.4.3**) although this was not observed under natural feeding conditions.

Environmental variables made little difference to observed feeding rates at the rich food patches which I

provided. These patches were potentially as predictable to predators as they were to Snow Buntings, and were therefore risky, if rich, feeding locations. Although predators were seen only rarely on Cairn Gorm (**4.4**), some species (notably Sparrowhawks) can develop fixed hunting patterns which may be reinforced by the presence of prey or hunting success (e.g. Wilson & Weir 1989). Snow Buntings left the area of the artificial feeding sites, often moving a considerable distance, when not feeding. This may have been because they considered these sites to be more dangerous than elsewhere, or it may have been a means of reducing the risk that predators would recognise the patches or develop more effective hunting stategies at these patches. Even slight increases in risk of predation can theoretically cause significant changes in feeding behaviour (McNamara & Houston 1990). Snow Buntings may therefore not be willing, even at times of high nutritional stress, to trade-off predator vigilance for higher intake rates at these relatively rich feeding patches, especially since the immediate threat of starvation is low (**8.4.1**) and they have the option of dispersal to another site. In this open-country species, early predator detection and avoidance, rather than escape to cover (Lima & Dill 1990), is probably critical for survival.

10.3 Factors affecting feeding efficiency and site fidelity

10.3a The importance of experience to feeding efficiency

One major finding of this thesis is the profound role that experience (both age- and site-related) had on feeding behaviour, leading to variation in energy reserves, and perhaps ultimately determining whether or not an individual remained faithful to its wintering site. Adults and/or birds with previous site experience had faster peck-rates in a given situation and, for a given flock-size, were more likely to spend most of their time feeding in the important early parts of feeding bouts. The time that inexperienced birds lost was mainly spent vigilant (**6.3.1**), either to the activities of predators or conspecifics. They were also more frequently found in feeding positions in the centre of flocks, and, in females, age and prior site experience was associated with feeding earlier and in larger flocks respectively. Birds were probably safest in central feeding positions in large flocks or after recent scanning (i.e. early in feeding bouts). This may have allowed them to reduce their vigilance levels and hence concentrate on feeding without suffering an increased risk of predation. Further, older birds remained in feeding positions for longer uninterrupted periods.

These advantages of experience are perhaps best explained by some combination of (i) more efficient vigilance behaviour, because experienced birds know when and where predators are most likely to appear, how they will attack, and how best to escape, (ii) more effective social behaviour, perhaps because known individuals are more readily tolerated, or less often tested by other resident birds, or (iii) better food handling ability. They *cannot*, however, be explained by a factor which is usually involved or intimated in such circumstances (see **6.1** & **7.1**), namely social dominance: juveniles, and to a lesser extent birds with little site experience, won more contests against their respective counterparts than expected. Any advantage

enjoyed by dominant birds presumably reduced the effects of age- or site-related experience. In other words, juveniles and inexperienced birds may have been forced to initiate aggressive encounters because their feeding would otherwise have been even more inefficient.

Although inexperience, rather than low rank, can explain lower peck-rates and reductions in the amount of time spent feeding, dominance perhaps helped explain why young and inexperienced females (but not males) were absent from (and were perhaps excluded from) the early parts of feeding bouts and large flock-sizes. Experience of feeding in social situations, perhaps partly as a result of feeding with familiar flock-mates, may have allowed adult and/or experienced females to join such favourable feeding environments more easily. It is not entirely clear, however, why juveniles and inexperienced birds (of both sexes) were dominant to their counterparts yet could not maintain central feeding positions, nor remain on the central arena as often as older birds. Perhaps inexperienced birds were more neophobic, either of the site or with such close feeding proximity to conspecifics (most natural flocks fed at much lower densities). Alternatively, they may have been less familiar with the dispersion of food throughout the central feeding arena, and less willing to risk moving to a more central position lest food availability, and hence their feeding rate, decreased.

10.3b A smaller influence of social dominance on feeding efficiency

As a result of the large difference in agonistic ability noted between the sexes (**7.3.3a**), it was perhaps inevitable that males would glean some foraging advantage in competitive situations, i.e. large dense flocks. The *extent* of the advantage is surprisingly low, however, especially because females are smaller and would require less energy for maintenance. Females with site-experience did not avoid feeding in large flocks, although they did tend to feed slightly later in feeding bouts than males. Although females in large flocks moved more than males (possibly because they were displaced), they did not move as much when in smaller groups, perhaps to avoid unnecessary interactions. They were not more likely than males to have left the arena at the end of a time budget, nor were they less likely to feed in central flock positions.

10.3c Male tolerance of females

Did males tolerate females to reduce their own risk of displacement? Although my data were inadequate to test whether males discriminated for or against females when choosing opponents (**7.4.2**), presumably it would be of benefit to foraging males to be surrounded by less aggressive females than fellow males (**7.3.1b, Figs.7.17 & 7.25**). These could provide a shield against attacks from other high-ranking individuals, and perhaps again allow a more favourable foraging-vigilance trade-off. Tolerance of familiar subordinates has been shown in Siskins (Senar *et al.* 1990a), and may benefit familiar subordinate Dark-eyed Juncos (Wiley 1990). In Snow Buntings, high turnover may reduce familiarity between individuals, hence favouring male tolerance of females generally, rather than particular individuals. This

requires that males could readily distinguish females, but this is unlikely to have been a problem because even my human eye could easily and quickly determine the sex of most Snow Buntings in the field. Less aggressive behaviour in females could be an adaptation to promoting 'peace' in feeding flocks, thus allowing females to take up and maintain richer or more central feeding positions. Aggression in males might be advantageous when conditions are severe and food is limited, thus favouring birds which assert their intersexual dominance. Access to food and the concept of tolerance deserve further study in relation to sex and/or dominance in this and other species.

10.3d Residency mediated through energy reserves

Despite the difficulties involved in interpreting body-mass data, the more efficient males, adults and experienced birds did appear to have greater fat or mass reserves (**8.3.4 & 8.3.10**). There was even indirect evidence that experienced birds were capable of conserving these reserves more effectively than their counterparts in bad weather (**8.3.10**). If the data are taken at face value, site-experience was more likely to be associated with elevated energy reserves than either gender or age (0.5-5.0g excess body-mass in experienced birds, **Table 8.5**; c0.5g excess in males and adults, **8.3.4 & 8.4.4**), although the latter were measured in birds with little site-experience and may have been affected by the hasty departure of birds with below-average energy reserves. Unfortunately, sample size and composition of masses registered on the electronic weighing balances were probably inadequate to conclusively state whether mass reserves, or the rate of change of these reserves, was related to dominance, age or sex in experienced birds. However, body mass had a strong positive effect on the likelihood that a newly-arrived bird would become established on Cairn Gorm.

Again site-experience was a major determinant of an individual's relative probability of being seen during snowy weather. This may have been directly due to greater fat reserves, or indirectly due to a greater ability to maintain reserves during adverse conditions. As well as the proposed benefits that site-experience confers on feeding efficiency, experienced birds presumably also have greater awareness of where food sources will be available during adverse weather.

10.3e How can dominance influence site fidelity between, but not within, genders?

There was no evidence that dominance directly affected residency after birds became established, but males were relatively more likely to be seen during snow than females, especially in the worst snowfalls. Why was there no dominance effect *within* sexes? Perhaps this was again related to the Snow Bunting's nomadic nature, its gregariousness and potentially large turnover rates. These characteristics would reduce the probability that birds recognise each other *individually*. Females, but not males, may have been penalised in competitive situations if males targeted females because they had a high probability of winning intersexual

encounters. Males may have been unable to identify low-rank males successfully (assuming plumage did not signal status accurately - unlikely given that dowdier, more female-like juvenile males had higher average rank than adult males), and therefore avoided intrasexual aggression at such times. Although this contrasts with the male-tolerance-of-females scenario described above, two different approaches to females might be expected depending on the males' foraging status: tolerate them if feeding at a profitable rate, but usurp them in more difficult conditions if they appeared to be feeding in a richer patch. Rohwer & Ewald (1981) described an analogous switch in behaviour of dominant Harris' Sparrows towards subordinates. If such a switch in male behaviour occurred, females may be pre-adapted to earlier emigration from a site in deteriorating conditions, giving a possible explanation for the apparent influence of dominance between the sexes, but not between individuals within sexes, on emigration during bad weather. Low numbers, and hence lack of competition for feeding spaces, may have allowed males to continue tolerating females even in bad weather during the latter winters of the study, thereby reducing the probability of differential dispersal away from Cairn Gorm during snow-bouts.

The main presumption of this explanation for differences in the degree of residency exhibited by male versus female Snow Buntings in the absence of a direct influence of individual dominance, is that birds are unable to accurately assess each other's **individual** dominance, because the numbers of conspecifics involved are too high. In Snow Buntings such a system could evolve through large turnover rates (remember that the artificial patches were much richer than natural patches and probably exerted a considerable negative influence on dispersal). In principle, changes in the pattern of aggressive behaviour could also occur in large flocks of more sedentary species. However, it might also be the case that the conditions likely to promote the change from tolerant to exploitive behaviours would also be likely to promote itinerant as opposed to sedentary behaviour.

10.3f Evolution of site fidelity

The importance of site-experience in improving feeding efficiency, allowing more effective control of body reserves, and hence enhancing an individual's ability to remain at a site in bad conditions is consistent with its role in the evolution of site fidelity (Gauthreaux 1982). Even in Snow Buntings, where under natural conditions at high altitudes the opportunities for site residency in winter would be low, many individuals showed an aptitude to become resident, and this was maintained under environmental conditions which would usually have forced birds to emigrate. The artificial, less-variable feeding regime which I provided on Cairn Gorm may have partially demonstrated how site-experience can change an itinerant nature to a more sedentary lifestyle. Experience at a site may be fundamental to many winter-resident bird species, promoting rapid winter settlement patterns and rigid adherence to that site after the choice was made. 'Normal' dominance patterns (site-, area- or age-related dominance effects, see **7.4.4**) may be of lesser fitness importance, i.e. secondary and more variable adaptations seen in some species because they further influence individual fitness. The costs of loss of dominance status may have less bearing on whether an

individual leaves its wintering site than loss of relevant site-related knowledge.

10.3g Comparisons with the Siskin

The studies by Senar and his co-workers on another nomadic species, the Siskin, provide an interesting contrast to my results and speculations outlined above. Senar *et al.* (1990b) found that dominance status was an important correlate of site fidelity in Siskins: resident birds tended to dominate transients. Despite this, males, which are dominant to females (Senar *et al.* 1990b), exhibit the same degree of site fidelity as females. Why should dominance status be more important to wintering Siskins than Snow Buntings, and, given that it is important, why does this not lead to an even greater intersexual difference in site fidelity than that observed in Snow Buntings?

One major difference between the species is that Siskins pair during winter (Senar 1985, Senar & Copete 1990). In some species dominant behaviour, even before the breeding season, may improve the chances of attracting a mate or the quality of that mate (e.g. Komers & Dhindsa 1989). Male Siskins may therefore benefit from attaining and advertising high status not only because winning contests enhances their immediate access to some contested resource, but because it may also improve their future breeding success. Consistent with this suggestion is the more elaborate display and submission behaviours noted in Siskins (Senar *et al.* 1990a), which perhaps allow honest assessment of fighting abilities while minimising more overtly costly aggressive behaviour (see Enquist *et al.* 1990). Also, Siskins appear to become increasingly tolerant of familiar conspecifics, perhaps allowing the formation of stable sub-flocks with stable social hierarchies (Senar *et al.* 1990a). Perhaps males are particularly tolerant or protective of their future mates. Dominant residents call to attract subordinate flock-mates, and hence gain food-finding or anti-predation benefits (Senar & Metcalfe 1988). Subordinates may also profit from the allegiance, although they often move on very soon afterwards (Senar *et al.* 1992a) suggesting that they face greater costs (due to high levels of aggression with other transients, and perhaps also predation) than residents if they stay. The greater mass of resident birds suggests that they benefit from their strategy, although transients may *choose* to maintain lower mass reserves to reduce predation risk or transport costs (Senar *et al.* 1992a). It is even possible that the costs of subordinance are reduced as a result of morphological differentiation and assortative mating amongst subordinates (Senar *et al.* 1994).

10.4 Reversals of dominance rank

The relatively low contribution of social dominance to feeding efficiency and site fidelity possibly explains how adult and experienced Snow Buntings can afford to be less dominant than younger birds or those with less site experience. Subordinance may help reduce energy expenditure by reducing active metabolic rate (Hogstad 1987), resting metabolic rate (Roskaft *et al.* 1986, Bryant & Newton 1994), or interaction rates (Jarvi & Bakken 1984). Other studies on northern biome animals (grouse and hares, see Thomas 1987)

have shown that winter behaviour is geared towards *conserving* energy. Adults and experienced birds, while maintaining higher feeding rates than their counterparts, may not be able to increase these rates further without incurring restrictive energetic or risk costs associated with dominance. Furthermore, as a result of their higher feeding success, they may not experience the deleterious stress effects usually associated with subordinance during difficult conditions (as indicated by increased corticosterone levels, e.g. Silverin *et al.* 1984, Schwabl *et al.* 1985). Increased aggression, resulting in apparently higher ranks, may simply indicate that juveniles, and to a lesser extent birds with little site experience, valued the contested feeding sites more than their counterparts. They were prepared to accept greater dominance costs because the importance of the reward was greater to them.

Presumably juveniles and birds with little site experience are less efficient foragers in other species too. However, site fidelity in other species may reduce the discrepancies between the age or experience groups earlier in the winter, or in more benign habitats than those experienced by Snow Buntings. Hence, the outcome of interactions may be less critical to a juvenile's immediate survival prospects. Moreover, if a species is site faithful, aggression and/or site defense may benefit adults by limiting the settlement of inferior competitors, reducing the probability that food resources become over-exploited. Such a strategy is perhaps compounded by the formation of strict territories and/or rank orders which promote increased acceptance of familiar individuals (e.g. territorial neighbours or group members), but vigorous rebuttal of strangers.

Thus in sedentary species accurate assertion and re-assertion of rank becomes more important. The long-term benefits of such assertions in nomadic species may be limited if group cohesion is low, and may not meet the time and energy costs of establishing dominance. Reduced aggressiveness towards young or inexperienced birds may enable incoming birds to remain at a feeding site with established birds despite poor initial feeding rates. The *benefits of flocking* then enable all birds to profit. As mentioned previously (**10.3g**), in nomadic species which pair or form cohesive sub-flocks, accurate *assertion of dominance* may again be expected. I would predict therefore that reversals of the usual dominance patterns are most likely where dominant behaviour is of relatively minor value, for instance amongst other highly mobile species which do not form pair bonds or individual allegiances in winter.

10.5 Enhancing our knowledge

This thesis has provided a rather broad-brush portrait of Snow Bunting ecology and behaviour in upland North-east Scotland, an approach which was necessary because little published information was available from such sites before my studies began. However, its wide-ranging remit may be its most worthwhile feature, because studies of mobile bird species are dismally scarce. The somewhat speculative nature of this resume underlines our rudimentary knowledge of the behavioural ecology of itinerant species. Although some of the more notable findings of this work, such as the heightened role of experience on foraging

efficiency and site fidelity, the influence of energy reserves on site-establishment, intersexual dominance effects in the absence of intrasexual effects, and the reversal of some anticipated dominance relationships, may not prove to be general to nomadic birds, hopefully they will have a place in future reviews of the behavioural ecology of itinerant species.

Unfortunately, the very nature of itinerant species makes them difficult to study since manipulations of their environment, even through provision of supplemental food, may change their residency patterns. This reduces the possibilities for making tight predictions under closely controlled conditions. Hopefully, however, this will not deter future workers from making general studies of such species, and attempting to grasp more specific opportunities when they occur.

REFERENCES

Adriansen, F. & Dhondt, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J. Anim. Ecol. 59: 1077-1090.

Alatalo, R.V., Gustafsson, L., & Lundberg, A. 1984. Why do young passerine birds have shorter wings than older birds? Ibis 126: 410-415.

Alerstam, T. 1990. Bird Migration. Cambridge University Press, Cambridge.

Alford, J.R.,III & Bolen, E.G. 1977. Influence of winter temperatures on Pintail sex ratios in Texas. Southwest. Nat. 21: 554-556.

Andersson, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. J. Anim. Ecol. 49: 175-184.

Andersson, S. & Ahlund, M. 1991. Hunger affects dominance among strangers in house sparrows. Anim. Behav. 41: 895-897.

Appleby, M.C. 1983. The probability of linearity in hierarchies. Anim. Behav. 31: 600-608.

Arcese, P. & Smith, J.N.M. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. J. Anim. Ecol. 54: 817-830.

Archawaranon, M., Dove, L. & Wiley, R.H. 1991. Social inertia and hormonal control of aggression and dominance in white-throated sparrows. Behaviour 118: 42-65.

Baker, M.C., Belcher, C.S., Deutsch, L.C., Sherman, G.L. & Thompson, D.B. 1981. Foraging success in Junco flocks and the effects of social hierarchy. Anim. Behav. 29: 137-142.

Baker, M.C. & Fox, S.F. 1978. Dominance, survival, and enzyme polymorphism in Dark-eyed Juncos, *Junco hyemalis*. Evolution 32: 697-711.

Balda, R.P. & Balda, J.H. 1978. The care of young Pinon Jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. J. Orn. 119: 146-171.

Baldassarre, G.A., Whyte, R.J. & Bolen, E.G. 1986. Body weight and carcass composition of non-breeding green-winged teal on the Southern High Plains of Texas. J. Wildl. Manage. 50: 420-426.

Balph, M.H. 1977. Winter social behaviour of dark-eyed juncos: communication, social organisation, and ecological implications. Anim. Behav. 25: 859-884.

Balph, M.H. 1979. Flock stability in relation to social dominance and agonistic behaviour in wintering Dark-eyed Juncos. Auk 96: 714-722.

Balph, M.H., Balph, D.F. & Romesburg, H.C. 1979. Social status signalling in winter flocking birds: an examination of a current hypothesis. Auk 96: 78-93.

Banks, K.W., Clark, H., Mackay, I.R.K., Mackay, S.G. & Sellers, R.M. 1989. Biometrics and pre-migratory fattening in the Snow Bunting *Plectrophenax nivalis*. Ring. & Migr. 10: 141-157.

Banks, K.W., Clark, H., Mackay, I.R.K., Mackay, S.G. & Sellers, R.M. 1990. Ageing, sexing and racing Snow Buntings in winter plumage. Ringers' Bulletin 7: 84-87.

Banks, K.W., Clark, H., Mackay, I.R.K., Mackay, S.G. & Sellers, R.M. 1991a. Origins, population structure and movements of Snow Buntings *Plectrophenax nivalis* wintering in Highland Region, Scotland. Bird Study 38: 10-19.

Banks, K.W., Clark, H., Mackay, I.R.K., Mackay, S.G. & Sellers, R.M. 1991b. Snow Buntings in Caithness. Scot. Birds 16: 57-65.

Baptista, L.F., Dewolfe, B.B. & Avery-Beausoleil, L. 1987. Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows. Wilson Bull. 99:86-91.

Barkan, C.P.L., Craig, J.L., Strahl, S.D., Stewart, A.M. & Brown, J.L. 1986. Social dominance in communal Mexican jays *Aphelocoma ultramarina*. Anim. Behav. 34: 175-187.

Barnard, C.J. 1980a. Equilibrium flock size and factors affecting arrival and departure in feeding house

sparrows. Anim. Behav. 28: 503-511.

Barnard, C.J. 1980b. Factors affecting flock size mean and variance in a winter population of house sparrows (*Passer domesticus* L.). Behaviour 74: 1-2.

Barnard, C.J. 1980c. Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). Anim. Behav. 28: 295-309.

Barnard, C.J. & Stephens, H. 1983. Costs and benefits of single and mixed-species flocking in fieldfares (*Turdus pilaris*) and redwings (*T. iliacus*). Behaviour 84: 91-123.

Barnard, C.J. & Thompson, D.B.A. 1985. Gulls and plovers: the ecology and behaviour of mixed-species feeding groups. Croom Helm, London.

Barnett, L.B. 1970. Seasonal changes in temperature acclimatisation of the House Sparrow *Passer domesticus*. Comp. Biochem. Physiol. 33: 559-578.

Bekoff, M. & Scott, A.C. 1989. Aggression, dominance, and social organization in evening grosbeaks. Ethology 83: 177-194.

Benkman, C.W. 1988. Flock size, food dispersion, and the feeding behavior of crossbills. Behav. Ecol. Sociobiol. 23: 167-175.

Bennett, J.W. & Bolen, E.G. 1978. Stress response in wintering green-winged teal. J. Wildl. Manage. 42: 81-86.

Berthold, P. 1984. The control of partial migration in birds: a review. The Ring 10: 253-265.

Bibby, C.J. 1986. Merlin. In: The atlas of wintering birds in Britain and Ireland. (ed. P. Lack). pp150-151. Poyser, Calton.

Biebach, H. 1983. Genetic determination of partial migration in the European robin (*Erithacus rubecula*). Auk 100: 601-606.

Black, J.M. & Owen, M. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. Anim. Behav. 37: 199-209.

Blem, C.R. 1990. Avian energy storage. In: Current Ornithology. Vol.7. (ed. D.M. Power). pp59-113. Plenum Press, New York.

Blem, C.R. & Shelor, M.H. 1986. Multiple regression analyses of midwinter fattening of the white-throated sparrow. Can. J. Zool. 64: 2405-2411.

Breuil, M. 1989. Les Oiseaux d'Islande - Ecologie et Biogeographie. R. Chabaud, Lechevalier, Paris.

Brown, J.L. 1975. The evolution of behaviour. Norton and Co., New York.

Brown, M.B. & Brown, C.R. 1988. Access to winter food resources to bright- versus dull-colored House Finches. Condor 90: 729-731.

Bryant, D.M. & Newton, A.V. 1994. Metabolic costs of dominance in dippers, *Cinclus cinclus*. Anim. Behav. 48: 447-455.

Buckland, S.T., Bell, M.V. & Picozzi, N. 1990. The Birds of North-east Scotland. North-east Scotland Bird Club, Aberdeen.

Burger, J. 1988. Effects of age on foraging in birds. Proc. Int. Ornithol. Congr. 19: 1127-1140.

Calder, W.A. 1974. Consequences of body size for avian energetics. In: Avian energetics. (ed. R.A. Paynter). Nuttall Ornithological Club Publ. No. 15. Cambridge, Massachusetts.

Caraco, T. 1979. Time budgeting and group size: a test of theory. Ecology 60: 618-627.

Caraco, T., Barkan, C., Beacham, J.L., Brisbin, L., Lima, S., Mohan, A., Newman, J.A., Webb, W., & Withiam, M.L. 1989. Dominance and social foraging: a laboratory study. Anim. Behav. 38: 41-58.

Caraco, T. & Lima, S.L. 1987. Survivorship, energy budgets and foraging risk. In: Quantative analyses of behaviour, Vol. 6, Foraging. (ed. M.L. Commons, A. Kacelnik, & S.J. Shettleworth). pp1-21. Lawrence Erlbaum, New Jersey.

Caraco, T., Martindale, S. & Pulliam, H.R. 1980. Avian flocking in the presence of a predator. Nature 285:

400-401.

Castro, G., Myers, J.P. & Ricklefs, R.E. 1992. Ecology and energetics of Sanderlings migrating to four latitudes. Ecology 73: 833-844.

Catterall, C.P., Kikkawa, J., & Gray, C. 1989. Inter-related age-dependent patterns of ecology and behaviour in a population of Silvereyes (Aves: Zosteropidae). J. Anim. Ecol. 58: 557-570.

Choudhury, S. & Black, J.M. 1991. Testing the behavioural dominance and dispersal hypothesis in Pochard. Ornis Scand. 22: 155-159.

Coulson, J.C., Monaghan, P., Butterfield, J., Duncan, N., Thomas, C. & Shedden, C. 1983. Seasonal changes in the Herring Gull in Britain: weight, moult and mortality. Ardea 71:235-244.

Cristol, D.A. 1992. Food deprivation influences dominance status in dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 43: 117-124.

Cristol, D.A., Nolan, V.,Jr. & Ketterson, E.D. 1990. Effect of prior residence on dominance status of dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 40: 580-586.

Cuadrado, M., Rodriguez, M. & Arjona, S. 1989. Fat and weight variations of Blackcaps wintering in southern Spain. Ring. & Migr. 10: 89-97.

Davidson, N.C. & Evans, P.R. 1982. Mortality of Redshanks and Oystercatchers from starvation during severe weather. Bird Study 29: 183-188.

Davies, N.B. 1976. Food, flocking and territorial behaviour of the pied wagtail (*Motacilla alba yarrelli* Gould) in winter. J. Anim. Ecol. 45: 235-253.

Davies, N.B. & Green, R.E. 1976. The development and ecological significance of feeding techniques in the reed warbler (*Acrocephalus scirpaceus*). Anim. Behav. 24: 213-229.

Davies, N.B. & Houston, A.I. 1984. Territory economics. In: Behavioural ecology: an evolutionary approach. 2nd edn. (eds. J.R. Krebs & N.B. Davies). pp148-169. Blackwell, Oxford.

Davis, P.G. 1981. Trapping methods for bird ringers. British Trust for Ornithology, Tring.

Dawson, W.R. & Marsh, R.L. 1986. Winter fattening in the American goldfinch and the possible role of temperature in its regulation. Pysiol. Zool. 59: 357-368.

Dearborn, D.C. & Wiley, R.H. 1993. Prior residence has a gradual influence on dominance in captive white-throated sparrows. Anim. Behav. 46: 39-46.

De Laet, J.F. 1985. Dominance and anti-predator behaviour of Great Tits *Parus major*: a field study. Ibis 127: 372-377.

Dementiev, G.P. & Gladkov, N.A. 1954. Birds of the Soviet Union, Vol. 5. English Translation (1970). Israel Programme for Scientific Translations, Jerusalem.

Desrochers, A. 1989. Sex, dominance, and microhabitat use in wintering Black-capped Chickadees: a field experiment. Ecology 70: 636-645.

Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. Anim. Behav. 43: 885-894.

Desrochers, A., Hannon, S.J. & Nordin, K.E. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105: 727-736.

Dhindsa, M.S., Komers, P.E. & Boag, D.A. 1989. The effect of familiarity with an environment on the dominance relationships between juvenile and adult Black-billed Magpies. Ornis Scand. 20: 187-192.

Diefenbach, D.R., Nichols, J.D. & Hines, J.E. 1988. Distribution patterns during winter and fidelity to wintering areas of American black ducks. Can. J. Zool. 66: 1506-1513.

Diefenbach, D.R., Derleth, E.L., Haegen, W.M.V., Nichols, J.D. & Hines, J.E. 1990. American Woodcock winter distribution and fidelity to wintering areas. Auk 107: 745-749.

Dougall, T.W. & Appleton, G.F. 1989. Winter weights and age stucture of a population of Pied Wagtails at a southern Scotland roost. Ring. & Migr. 10: 83-88.

Dugan, P.J., Evans, P.R., Goodyer, L.R. & Davidson, N.C. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. Ibis 123: 359-363.

Duncan, K. & Marquiss, M. 1993. The sex/age ratio, diving behaviour and habitat use of Goldeneye *Bucephala clangula* wintering in northeast Scotland. Wildfowl 44: 111-120.

Eden, S.F. 1987. Dispersal and competitive ability in the magpie: an experimental study. Anim. Behav. 35: 764-772.

Eden, S.F. 1989. The social organisation of non-breeding Magpies *Pica pica*. Ibis 131: 141-153.

Ekman, J. 1979. Coherence, composition and territories of winter social groups of the Willow Tit *Parus montanus* and the Crested Tit *P. cristatus*. Ornis Scand. 10: 56-68.

Ekman, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). J. Anim. Ecol. 53: 119-134.

Ekman, J. 1989. Ecology of non-breeding social systems of *Parus*. Wilson Bull. 101: 263-288.

Ekman, J. 1990. Alliances in winter flocks of willow tits; effects of rank on survival and reproductive success in male-female associations. Behav. Ecol. Sociobiol. 26: 239-245.

Ekman, J., Cederholm, G., & Askenmo, C. 1981. Spacing and survival in winter groups of Willow Tit *Parus montanus* and Crested Tit *P. cristatus* - a removal study. J. Anim. Ecol. 50: 1-9.

Ekman, J.B. & Hake, M.K. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behav. Ecol. 1: 62-67.

Ekman, J.B. & Lilliendahl, K. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. Behav. Ecol. 4: 232-238.

Elgar, M.A. 1987. Food intake rate and resource availability: flocking decisions in house sparrows. Anim Behav. 35: 1168-1176.

Elgar, M.A., Burren, P.J. & Posen, M. 1984. Vigilance and perception of flock size in foraging House Sparrows (*Passer domesticus* L.). Behaviour 90: 215-223.

Enoksson, B. 1988. Age- and sex-related differences in dominance and foraging behaviour of nuthatches (*Sitta europaea*). Anim. Behav. 36: 231-238.

Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. Anim. Behav. 40: 1-14.

Ens B.J. & Goss-Custard J.D. 1984. Interference among oystercatchers, *Haemotopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. J. Anim. Ecol. 53: 217-231.

Evans, P.R. 1981. Migration and dispersal of shorebirds as a survival strategy. In: Feeding and survival strategies in esturine organisms (eds. Jones & Wolff). pp275-290. Plenum Press, New York.

Feare, C.J. & Inglis, I.R. 1979. The effects of reduction of feeding space on the behaviour of captive Starlings *Sturnus vulgaris*. Ornis Scand. 10: 42-47.

Fleischer, R.C. 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging, and vigilance behaviour. Condor 85: 22-29.

Fox, A.D., King, R. & Watkin, J. 1992. Seasonal variation in weight, body measurements and condition of free-living Teal. Bird Study 39: 53-62.

Fretwell, S. 1968. Habitat distribution and survival in the Field Sparrow (*Spizella pusilla*). Bird-Banding 39: 293-306.

Fretwell, S. 1969. Dominance behaviour and winter habitat distribution in Juncos (*Junco hyemalis*). Bird-Banding 40: 1-25.

Fuller, R.J. 1986. Lapwing. In: The atlas of wintering birds in Britain and Ireland. (ed. P. Lack). pp188-189. Poyser, Calton.

Gauthreaux, S.A.,Jr. 1978. The ecological significance of behavioural dominance. In: Perspectives in Ethology. (eds. P.P.G. Bateson & P.H. Klopper). pp17-54. Plenum Press, New York.

Gauthreaux, S.A.,Jr. 1982. The ecology and evolution of avian migration systems. In: Avian Biology, Vol. 6. (eds. D.S. Farner, J.R. King & K.C. Parkes). pp93-168. Academic Press, New York.

Gauthreaux, S.A.,Jr. 1988. Age effects on migration and habitat selection. Proc. Int. Ornithol. Congr. 19: 1106-1115.

Gochfeld, M. & Burger, J. 1984. Age differences in foraging behavior of the American Robin (*Turdus migratorius*). Behaviour 88: 227-239.

Goldman, P. 1980. Flocking as a possible predator defense in Dark-eyed Juncos. Wilson Bull. 92: 88-95.

Goss-Custard, J.D. 1976. Variation in the dispersion of Redshank *Tringa totanus* on their winter feeding grounds. Ibis 118: 257-263.

Goss-Custard, J.D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (*Charadrii*). J. Appl. Ecol. 14: 721-739.

Goss-Custard, J.D. 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit. 1984. Rates of food intake and aggression of oystercatchers, *Haemotopus ostralegus*, on the most and least preferred mussel, *Mytilus edulis*, beds on the Exe estuary. J. Anim. Ecol. 53: 233-245.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit. 1987. Age-related effects in oystercatchers, *Haemotopus ostralegus*, feeding on mussels, *Mytilus edulis*. II. Aggression. J. Anim. Ecol. 56: 537-548.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit. 1991. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Grant, B.R. & Grant, P.R. 1989. Natural selection in a population of Darwin's Finches. Am. Nat. 133: 377-393.

Green, R.E. 1986. Skylark. In: The atlas of wintering birds in Britain and Ireland. (ed. P. Lack). pp290-291. Poyser, Calton.

Greig, S.A., Coulson, J.C. & Monaghan, P. 1985. Feeding strategies of male and female adult herring gulls (*Larus argentatus*). Behaviour 94: 41-59.

Groves, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behaviour. Auk 95: 95-103.

Grubb, T.C.,Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. Auk 106: 314-320.

Gudmundsson, G.A., Lindstrom, A. & Alerstam, T. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. Ibis 133: 140-152.

Haftorn, S. 1989. Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. Wilson Bull. 101: 217-235.

Hake, M. & Ekman, J. 1988. Finding and sharing depletable patches: when group foraging decreases intake rates. Ornis Scand. 19: 275-279.

Harrington, B.A. & Groves, S. 1977. Aggression in foraging migrant Semipalmated Sandpipers. Wilson Bull. 89: 336-338.

Heavisides, A. 1987. British and Irish Merlin recoveries, 1911-1984. Ring. & Migr. 8: 29-41.

Heiniger, P.H. 1991. Anpassungsstrategien des Schneefinken *Montifringilla nivalis* an die extremen Umweltbedingungen des Hochgebirges. Orn. Beob. 88: 193-207.

Helms, C.W. & Drury, W.H.,Jr. 1960. Winter and migratory weight and fat: field studies on some North American buntings. Bird-Banding 31: 1-40.

Henty, C.J. 1979. The foraging activity of Snow Buntings wintering inland in Scotland. Bird Study 26: 192-194.

Hepp, G.R. 1989. Benefits, costs and determinants of dominance in American black ducks. Behaviour 110:

222-234.

Heppleston, P.B. 1970. Anatomical observations on the bill of the oystercatcher (*Haematopus ostralegus*) in relation to feeding behaviour. J. Zoo. Soc. London 161: 519-524.

Hillcoat, R. 1962. Snow Buntings 3,600 feet up Cairngorm in Christmas and New Year weekend. Scot. Birds 2: 108.

Hogstad, O. 1987. It is expensive to be dominant. Auk 104: 333-336.

Hogstad, O. 1988a. Advantages of social foraging of Willow Tits *Parus montanus*. Ibis 130: 275-283.

Hogstad, O. 1988b. Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. Ornis Scand. 19: 169-174.

Hogstad, O. 1988c. Social rank and anti-predator behaviour of Willow Tits *Parus montanus* in winter flocks. Ibis 130: 45-56.

Hogstad, O. 1988d. The influence of energy stress on social organisation and behaviour of Willow Tits *Parus montanus*. Fauna norv. Ser. C., Cinclus 11: 89-94.

Hogstad, O. 1989a. Subordination in mixed-age bird flocks - a removal study. Ibis 131: 128-134.

Hogstad, O. 1989b. The role of juvenile willow tits, *Parus montanus*, in the regulation of winter flock size: an experimental study. Anim. Behav. 38: 920-925.

Hogstad, O. 1991. The effect of social dominance on foraging by the Three-toed Woodpecker *Picoides tridactylus*. Ibis 133: 271-276.

Holberton, R.L., Hanano, R. & Able, K.P. 1990. Age-related dominance in male dark-eyed juncos: effects of plumage and prior residence. Anim. Behav. 40: 573-579.

Holmes, R.T. 1976. Body composition, lipid reserves and caloric densities of summer birds in a northern deciduous forest. Am. Midl. Nat. 96: 281-290.

Horvath, E.G. & Sullivan, K.A. 1988. Facultative migration in Yellow-eyed Juncos. Condor 90: 482-484.

Hotker, H. 1989. Sex ratios and weights of Meadow Pipits *Anthus pratensis* in their winter quarters. Ring. & Migr. 10: 124-132.

Houston, A.I. & McNamara, J.M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. Anim. Behav. 36: 166-174.

Houston, A.I. & McNamara, J.M. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. Ornis Scand. 24: 205-219.

Huntingford, F.A. & Turner, A.K. 1987. Animal conflict. Cambridge University Press, Cambridge.

Inman, A.J. 1990. Group foraging in starlings: distributions of unequal competitors. Anim. Behav. 40: 801-810.

Jackson, W.M. 1991. Why do winners keep winning? Behav. Ecol. Sociobiol. 28: 271-276.

Jackson, W.M., Rohwer, S. & Winnegrad, R.L. 1988. Status signalling is absent within age-and-sex classes of Harris' Sparrows. Auk 105: 424-427.

Jansen, A. 1990. Acquisition of foraging skills by Heron Island Silvereyes *Zosterops lateralis chlorocephala*. Ibis 132: 95-101.

Jansson, C., Ekman, J. & Bromssen van, A. 1981. Winter mortality and food supply in tits *Parus* spp. Oikos 37: 313-322.

Jarvi, T. & Bakken, M. 1984. The function of the variation in the breast stripe of the Great Tit, *Parus major*. Anim. Behav. 32: 590-596.

Jenni, L. 1993. Structure of a Brambling *Fringilla montifringilla* roost according to sex, age and body-mass. Ibis 135: 85-90.

Jenni, L. & Jenni-Eiermann, S. 1987. Body weight and energy reserves of Bramblings in winter. Ardea 75: 271-284.

Jennings, T., & Evans, S.M. 1980. Influence of position in the flock and flock-size on vigilance in the

starling (*Sturnus vulgaris*). Anim. Behav. 28: 634-635.

Jukema, J. & Fokkema, J. 1992. Herkomst van in Nederland overwinterende Sneeuwgorzen *Plectrophenax nivalis*. Limosa 65: 67-72.

Kauffmann, J.H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. 58: 1-20.

Kendeigh, S.C. 1969. Tolerance of cold and Bergmann's Rule. Auk 86: 13-25.

Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. Condor 72: 60-65.

Kennedy, M. & Gray, R.D. 1994. Agonistic interactions and the distribution of foraging organisms: individual costs and social information. Ethology 96: 155-165.

Kerlinger, P. & Lein, M.R. 1986. Differences in winter range among age-sex classes of Snowy Owls *Nyctea scandiaca* in North America. Ornis Scand. 17: 1-7.

Ketterson, E.D. 1978. Environmental influences upon aggressive behaviour in wintering juncos. Bird-Banding 49: 313-320.

Ketterson, E.D. 1979a. Aggressive behaviour in wintering Dark-eyed Juncos: determinants of dominance and their possible relationship to geographic variation in sex ratio. Wilson Bull. 91: 371-383.

Ketterson, E.D. 1979b. Status signalling in Dark-eyed Juncos. Auk 96: 94-99.

Ketterson, E.D. & Nolan, V.,Jr. 1976. Geographic variation and its climatic correlates in the sex-ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology 57: 679-693.

Ketterson, E.D. & Nolan, V.,Jr. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. Auk 99: 243-259.

Ketterson, E.D. & Nolan, V.,Jr. 1983. The evolution of differential bird migration. In: Current Ornithology, Vol. 1. (ed. R.F. Johnston). pp357-402. Plenum Press, New York.

Ketterson, E.D. & Nolan, V.,Jr. 1985. Intraspecific variation in avian migration: evolutionary and regulatory aspects. In: Migration: mechanisms and adaptive significance. (ed. M.A. Rankin). pp553-579. Un. of Texas Contributions in Marine Science Supp. 27.

Keys, G.C. & Rothstein, S.I. 1991. Benefits and costs of dominance and subordinance in white-crowned sparrows and the paradox of status signalling. Anim. Behav. 42: 899-912.

Kikkawa, J. 1980. Winter survival in relation to dominance classes among Silvereyes *Zosterops lateralis chlorocephala* of Heron Island, Great Barrier Reef. Ibis 122: 437-446.

King, J.R. & Farner, D.S. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. Amer. Nat. 100: 403-418.

King, J.R., Farner, D.S. & Mewaldt, L.R. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelli*. Condor 67: 489-504.

Koivula, K., Lahti, K., Orell, M. & Rytkonen, S. 1993. Prior residency as a key determinant of social dominance in the willow tit (*Parus montanus*). Behav. Ecol. Sociobiol. 33: 283-287.

Komers, P.E. 1989. Dominance relationships between juvenile and adult black-billed magpies. Anim. Behav. 37: 256-265.

Komers, P.E. & Dhindsa, M.S. 1989. Influence of dominance and age on mate choice in black-billed magpies: an experimental study. Anim. Behav. 37: 645-655.

Komers, P.E. & Komers, E.J. 1992. Juvenile male magpies dominate adults irrespective of size differences. Can. J. Zool. 70: 815-819.

Krementz, D.G., Hines, J.E., Corr, P.O. & Owen, R.B.,Jr. 1989. The relationship between body mass and annual survival in American Black Ducks. Ornis Scand. 20: 81-85.

Lack, P. 1986. The atlas of wintering birds in Britain and Ireland. Poyser, Calton.

Lambert, R. 1986. Snow Bunting. In: The atlas of wintering birds in Britain and Ireland. (ed. P. Lack).

pp410-411. Poyser, Calton.

Lehikoinen, E. 1986. Is fat fit? - a field study of survival and fatness in the Great Tit, *Parus major* L. Ornis Fennica 63: 112-119.

Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. Ornis Scand. 18: 216-226.

Lehikoinen, E. & Hakala, J. 1988. Variation in weight of migratory Dippers *Cinclus cinclus* in their Finnish winter quarters. Bird Study 35: 101-108.

Lemel, J. & Wallin, K. 1993. Status signalling, motivational condition and dominance: an experimental study in the great tit, *Parus major* L. Anim. Behav. 45: 549-558.

Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67: 377-385.

Lima, S.L. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. Behaviour 104: 231-238.

Lima, S.L. 1988a. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53: 3-11.

Lima, S.L. 1988b. Vigilance during the initiation of daily feeding in dark-eyed juncos. Oikos 53: 12-16.

Lima, S.L. & Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619-640.

Lindstrom, A., Hasselquist, D., Bensch, S. & Grahn, M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. Anim. Behav. 40: 453-461.

Loria, D.E. & Moore, F.R. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. Behav. Ecol. 1: 24-35.

Lundberg, P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. Behav. Ecol. Sociobiol. 17: 185-189.

Lundberg, P. 1987. Partial bird migration and evolutionary stable strategies. J. Theor. Biol. 125: 351-360.

Lyon, B.E. & Montgomerie, R.D. 1986. Delayed plumage maturation in passerine birds: reliable signalling by dishonest males? Evolution 40: 605-615.

Marchetti, K. & Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol. Rev. 64: 51-70.

Marquiss, M. 1980. Habitat and diet of male and female Hen Harriers in Scotland in winter. Brit. Birds 73: 555-560.

Mayhew, P. & Houston, D. 1989. Feeding site selection by Wigeon *Anas penelope* in relation to water. Ibis 131: 1-8.

McNab, B.K. 1971. On the ecological significance of Bergmann's Rule. Ecology 52: 845-854.

McNamara, J.M. & Houston, A.I. 1986. The common currency for behavioural decisions. Am. Nat. 127: 358-378.

McNamara, J.M. & Houston, A.I. 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheor. 38: 37-61.

Mearns, R. 1982. Winter occupation of breeding territories and winter diet of Peregrines in South Scotland. Ornis Scand. 13: 79-83.

Meltofte, H. 1983. Arrival and pre-nesting period of the Snow Bunting *Plectophenax nivalis* in East Greenland. Polar Research 1: 185-198.

Metcalfe, N.B. 1986. Variation in winter flocking associations and dispersion patterns in the turnstone *Arenaria interpres*. J. Zool., Lond. (A) 209:: 385-403.

Metcalfe, N.B. & Furness, R.W. 1985. Survival, winter population stability and site fidelity in the turnstone. Bird Study 32: 207-214.

Metcalfe, N.B. & Furness, R.W. 1987. Aggression in shorebirds in relation to flock density and composition. Ibis 129: 553-563.

Moller, A.P. 1987a. Social control of deception among status signalling house sparrows *Passer domesticus*. Behav. Ecol. Sociobiol. 20: 307-311.

Moller, A.P. 1987b. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. Anim. Behav. 35: 1637-1644.

Moller, A.P. 1988. Badge size in the house sparrow *Passer domesticus*. Effects of intra- and intersexual selection. Behav. Ecol. Sociobiol. 22: 373-378.

Mulvihill, R.S. & Chandler, C.R. 1991. A comparison of wing-shape between migratory and sedentary dark-eyed juncos (*Junco hyemalis*). Condor 93: 172-175.

Muma, K.E. & Weatherhead, P.J. 1991. Plumage variation and dominance in captive female Red-winged Blackbirds. Can. J. Zool. 69: 49-54.

Myers, J.P. 1981a. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Can. J. Zool. 59: 1527-1534.

Myers, J.P. 1981b. Cross-seasonal interactions in the evolution of sandpiper social systems. Behav. Ecol. Sociobiol. 8: 195-202.

Nethersole-Thompson, D. 1966. The Snow Bunting. Oliver & Boyd, Edinburgh and London.

Newton, I. 1972. Finches. Collins, London.

Newton, I. (ed.) 1989. Lifetime reproduction in birds. Academic Press, London.

Newton, I., Wyllie, I. & Mearns, R. 1986. Spacing of Sparrowhawks in relation to food supply. J. Anim. Ecol. 55: 361-370.

Nichols, J.D., Reinecke, K.J. & Hines, J.E. 1983. Factors affecting the distribution of mallards wintering in the Mississippi Alluvial Valley. Auk 100: 932-946.

Nilsson, J.-A. 1989. Establishment of juvenile marsh tits in winter flocks: an experimental study. Anim. Behav. 38: 586-595.

Nisbet, I.C.T. & Medway, Lord 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. Ibis 114: 451-493.

Nolan, V.,Jr. & Ketterson, E.D. 1983. An analysis of body mass, wing length and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. Wilson Bull. 95: 603-620.

Nolan, V.,Jr. & Ketterson, E.D. 1991. Experiments on winter-site attachment in young dark-eyed juncos. Ethology 87: 123-133.

Norberg, U.M. 1989. Vertebrate flight: Mechanics, physiology, morphology, ecology and evolution. Springer-Verlag, Berlin.

Norusis, M.J. 1986a. SPSS/PC+. SPSS INC, Chicago.

Norusis, M.J. 1986b. SPSS/PC+ Advanced Statistics. SPSS Inc, Chicago.

Oberski, I.M. & Wilson, J.D. 1991. Territoriality and site-related dominance: on two related concepts in avian social organisation. Ethology 87: 225-236.

Ornat, A.L. & Greenberg, R. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. Auk 107: 539-543.

Owen, M. & Dix, M. 1986. Sex ratios in some common British wintering ducks. Wildfowl 37: 104-112.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behaviour. J. Theor. Biol. 47: 223-243.

Partridge, L. 1978. Habitat selection. In: Behavioural ecology: an evolutionary approach. 1st edn. (eds. J.R. Krebs & N.B. Davies). pp351-376. Blackwell Scientific Press, Oxford.

Partridge, L. & Green, P. 1985. Intraspecific feeding specialisations and population dynamics. In: Behavioural ecology: ecological consequences of adaptive behaviour. (eds. R.M. Sibly & R.H.

Smith). pp207-226. Blackwell, Oxford.

Pattenden, R.K. & Boag, D.A. 1989. Skewed sex ratio in a northern wintering population of mallards. Can. J. Zool. 67: 1084-1087.

Payevsky, V.A. 1994. Age and sex structure, mortality and spatial winter distribution of Siskins (*Carduelis spinus*) migrating through eastern Baltic area. Vogelwarte 37: 190-198.

Peach, W.J. & Fowler, J.A. 1989. Movements of wing-tagged Starlings *Sturnus vulgaris* from an urban communal roost in winter. Bird Study 36: 16-22.

Peach, W.J., Hodson, D.P. & Fowler, J.A. 1992. Variation in the winter body mass of starlings *Sturnus vulgaris*. Bird Study 39: 89-95.

Pearson, S.M. 1989. Food patches and foraging group size in granivorous birds. Anim. Behav. 38: 665-674.

Pearson, S.M. 1991. Food patches and the spacing of individual foragers. Auk 108: 355-362.

Percival, S.M. 1991. The population structure of Greenland Barnacle Geese *Branta leucopsis* on the wintering grounds on Islay. Ibis 133: 357-364.

Piper, W.H. 1990. Exposure to predators and access to food in wintering white-throated sparrows *Zonotrichia albicollis*. Behaviour 112: 284-298.

Piper, W.H. & Wiley, R.H. 1989. Correlates of dominance in wintering white-throated sparrows: age, sex and location. Anim. Behav. 37: 298-310.

Piper, W.H. & Wiley, R.H. 1990a. Correlates of range size in wintering white-throated sparrows, *Zonotrichia albicollis*. Anim. Behav. 40: 545-552.

Piper, W.H. & Wiley, R.H. 1990b. The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*). Behav. Ecol. Sociobiol. 26: 201-208.

Popp, J.W. 1987a. Resource value and dominance among American goldfinches. Bird Behaviour 7: 73-77.

Popp, J.W. 1987b. Risk and effectiveness in the use of agonistic displays by American goldfinches. Behaviour 103: 141-156.

Post, W. 1992. Dominance and mating success in male boat-tailed grackles. Anim. Behav. 44: 917-929.

Powell, G.V.N. 1974. Experimental analysis of the social value of flocking by Starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav. 22: 501-505.

Poysa, H. 1987. Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. Behaviour 103: 108-122.

Prescott, D.R.C. 1991. Winter distribution of age and sex classes in an irruptive migrant, the Evening Grosbeak (*Coccothraustes vespertinus*). Condor 93: 694-700.

Prys-Jones, R. 1984. Migration patterns of the Reed Bunting, *Emberiza schoeniclus schoeniclus*, and the dependence of wintering distribution on environmental conditions. Le Gerfaut 74: 15-37.

Pulliam, H.R., Anderson, K.A., Misztal, A. & Moore, N. 1974. Temperature-dependent social behaviour in Juncos. Ibis 116: 360-364.

Pulliam, H.R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: Behavioral ecology: an evolutionary approach. 2nd edn. (eds. J.R. Krebs & N.B. Davies). pp122-147. Blackwell, Oxford.

Pulliam H.R. & Enders, F. 1971. The feeding ecology of five sympatric finch species. Ecology 52: 557-566.

Pulliam, H.R. & Millikan, G.C. 1982. Social organization in the nonreproductive period. In: Avian biology. Vol. 6. (eds. D.S. Farner, J.R. King & K.C. Parkes). pp169-197. Academic Press, New York.

Pulliam, H.R. & Parker, T.A. 1979. Population regulation of sparrows. Fortschr. Zool. 25: 137-147.

Puttick, G.M. 1981. Sex-related differences in foraging behaviour of Curlew Sandpipers. Ornis Scand. 12: 13-17.

Rabenold, K.N. & Rabenold, P.P. 1985. Variation in altitudinal migration, winter segregation, and site

tenacity in two subspecies of Dark-eyed Juncos in the southern Apalachians. Auk 102: 805-819.

Rae, R. 1986. Clap-netting Snow Buntings. Ringers' Bulletin 6: 116.

Rae, R. & Marquiss, M. 1989. Ageing and sexing of Snow Buntings wintering on the Aberdeenshire coast, their biometrics and sex ratio. Ring. & Migr. 10: 133-140.

Ramenofsky, M., Gray, J.M. & Johnson, R.B. 1992. Behavioural and physiological adjustments of birds living in winter flocks. Ornis Scand. 23: 371-380.

Rappole, J.H., Ramos, M.A. & Winker, K. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. Auk 106: 402-410.

Rayner, J.M.V. 1988. Form and function in avian flight. Curr. Ornithol. 5: 1-66.

Real, L.A. & Caraco, T. 1986. Risk and foraging in stochastic environments: theory and evidence. Ann. Rev. Ecol. Syst. 15: 393-425.

Richner, H. 1989. Phenotypic correlates of dominance in carrion crows and their affects on access to food. Anim. Behav. 38: 606-612.

Rogers, C.M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? Ecology 68: 1051-1061.

Rogers, C.M. & Rogers, C.J. 1990. Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. Ornis Scand. 21: 105-114.

Rogers, C.M., Smith, J.N.M., Hochachka, W.M., Cassidy, A.L.E.V., Taitt, M.J., Arcese, P. & Schluter, D. 1991. Spatial variation in winter survival of Song Sparrows *Melospiza melodia*. Ornis Scand. 22: 387-395.

Rogers, C.M., Theimer, T.L., Nolan, V.Jr. & Ketterson, E.D. 1989. Does dominance determine how far dark-eyed juncos, *Junco hyemalis*, migrate into their winter range? Anim. Behav 37: 498-506.

Rohwer, S. 1977. Status signalling in Harris Sparrows: some experiments in deception. Behaviour 61: 107-129.

Rohwer, S. & Butcher, G.S. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. Am. Nat. 131: 556-572.

Rohwer, S. & Ewald, P.W. 1981. The cost of dominance and advantage of subordination in a badge signaling system. Evolution 35: 441-454.

Rohwer, S., Ewald, P.W. & Rohwer, F.C. 1981. Variation in size, appearance and dominance within and among the sex and age classes of Harris' Sparrows. J. Field Ornithol. 52: 291-303.

Rohwer, S. & Rohwer, F.C. 1978. Status signalling in Harris' sparrows: experimental deceptions achieved. Anim. Behav. 26: 1012-1022.

Roskaft, E., Jarvi, T., Bakken, M., Bech, C. & Reinertsen, R.E. 1986. The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Anim. Behav. 34: 838-842.

Saino, N. 1994. Time budget variation in relation to flock size in carrion crows, *Corvus corone corone*. Anim. Behav. 47: 1189-1196.

Sasvari, L. 1992. Great tits benefit from feeding in mixed-species flocks: a field experiment. Anim. Behav. 43: 289-296.

Schneider, K.J. 1984. Dominance, predation and optimal foraging in White-throated Sparrow flocks. Ecology 65: 1820-1827.

Schwabl, H., Ramenofsky, M., Schwabl-Benzinger, I., Farner, D.S. & Wingfield, J.C. 1988. Social status, circulating levels of hormones and competition for food in winter flocks of the White-throated Sparrow. Behaviour 107: 107-121.

Schwabl, H., Wingfield, J.C. & Farner, D.S. 1985. Influence of winter on endocrine state and behaviour in European blackbirds (*Turdus merula*). Z. Tierpsychol. 68: 244-252.

Searcy, W.A. 1979. Morphological correlates of dominance in captive male Red-winged Blackbirds. Condor 81: 417-420.

Senar, J.C. 1985. Interactional rules in captive Siskins (*Carduelis spinus*). Misc. Zool. 9: 347-360.

Senar, J.C., Burton, P.J.K. & Metcalfe, N.B. 1992a. Variation in the nomadic tendency of a wintering finch, *Carduelis spinus* and its relationship with body condition. Ornis Scand. 23: 63-72.

Senar, J.C., Camerino, M. & Metcalfe, N.B. 1989. Agonistic interactions in siskin flocks: why are dominants sometimes subordinate? Behav. Ecol. Sociobiol. 25: 141-145.

Senar, J.C., Camerino, M. & Metcalfe, N.B. 1990a. Familiarity breeds tolerance: the development of social stability in flocking Siskins (*Carduelis spinus*). Ethology 85: 13-24.

Senar, J.C., Camerino, M. & Metcalfe, N.B. 1992b. Fighting as a subordinate in finch flocks: escalation is effective but risky. Anim. Behav. 43: 862-864.

Senar, J.C. & Copette, J.L. 1990. Observación de alimentación de cortejo en Lúganos *Carduelis spinus* invernantes. But. G.C.A. 7:11-12.

Senar, J.C., Copette, J.L. & Metcalfe, N.B. 1990b. Dominance relationships between resident and transient wintering siskins. Ornis Scand. 21: 129-132.

Senar, J.C., Lleonart, J. & Metcalfe, N.B. 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. J. Avian Biol. 25: 50-54.

Senar, J.C. & Metcalfe, N.B. 1988. Differential use of local enhancement for finding food by resident and transient Siskins. Anim. Behav. 36: 1549-1550.

Silverin, B., Viebke, P.-A. & Westin, J. 1984. Plasma levels of luteinizing hormone and steroid hormones in free-living winter groups of willow tits (*Parus montanus*). Hormones and Behavior 18: 367-379.

Sims, R.W. 1955. The morphology of the head of the Hawfinch. Bull. Brit. Mus. Nat. Hist. 2: 369-393.

Slagsvold, T. 1982. Criteria for estimating the condition of birds - relationship between fat content and body size dimensions in the hooded crow *Corvus corone cornix*. Ornis Scand. 13: 141-144.

Slotow, R., Alcock, J. & Rothstein, S.I. 1993. Social status signalling in white-crowned sparrows: an experimental test of the social control hypothesis. Anim. Behav. 46: 977-989.

Smith, J.N.M., Arcese, P. & Schluter, D. 1986. Song Sparrows grow and shrink with age. Auk 103: 210-212.

Smith, R.D. 1991. Monitoring of breeding Snow Buntings in 1988 and 1989. In: Britain's Birds in 1989-90: The conservation and monitoring review. (eds. D. Stroud & D. Glue). pp112-113. BTO/NCC, Stretford.

Smith, R.D. 1993. Snow Bunting. In: The new atlas of breeding birds in Britain and Ireland: 1988-1991. (eds. D.W. Gibbons, J.B. Reid, & R.A. Chapman). pp430-431. Poyser, London.

Smith, R.D. 1994. Snow buntings breeding in the Cairngorms: population dynamics and the influence of recreation. Scottish Natural Heritage Review No. 1.

Smith, R.D. & Marquiss, M. In press a. Breeding seasons and nesting success of Snow Buntings in North-east Scotland. Scot. Birds.

Smith, R.D. & Marquiss, M. In press b. Production and costs of nesting attempts in Snow Buntings: why do they attempt second broods? Ibis.

Smith, R.D., Marquiss, M., Whitfield D.P. & Thompson, D.B.A. 1993. Snow Buntings in Scotland: an update 1993. In: The snow bunting. 2nd edn. (D. Nethersole-Thompson). pp310-318. Peregrine Books, Leeds.

Smith, S.M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93: 95-107.

Smith, S.M. 1984. Flock switching in chickadees: why be a winter floater? Am. Nat. 123: 81-98.

Snow, D.W. 1968. Movements and mortality of British Kestrels. Bird Study 15: 65-83.

Snyder, N.F.R. & Wiley, J.W. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. Freeman & Co., San Francisco.

Spaans, A.L. 1977. Are starlings faithful to their individual winter quarters? Ardea 64: 83-87.

Stephens, D.W. & Krebs, J.R. 1986. Foraging Theory. Princeton University Press, Princeton.

Stevens, J. 1985. Foraging success of adult and juvenile Starlings (*Sturnus vulgaris*): a tentative explanation for the preference for cherries. Ibis 127: 341-347.

Sullivan, K.A. 1984. The advantages of social foraging in downy woodpeckers. Anim. Behav. 32: 16-22.

Summers, R.W., Strann, K.-B., Rae, R. & Heggas, J. 1990. Wintering Purple Sandpipers *Calidris maritima* in Troms county, northern Norway. Ornis Scand. 21: 248-254.

Sutherland, W.J., Jones, D.W.F. & Hadfield, R.W. 1986. Age differences in the feeding ability of Moorhens *Gallinula chloropus*. Ibis 128: 414-418.

Sutherland, W.J. & Parker, G.A. 1985. Distribution of unequal competitors: In: Behavioural ecology: ecological consequences of adaptive behaviour. (eds. R.M. Sibly & R.H. Smith). pp255-274. Blackwell, Oxford.

Svensson, L. 1984. Identification guide to European passerines. 3rd edn. Stockholm.

Swanson, D.L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). Auk 107: 561-566.

Swanson, D.L. 1992. Seasonal population dynamics of Dark-eyed Juncos from western Oregon. J. Field Ornithol. 63: 268-275.

Swingland, I.R. 1975. The influence of weather and individual interactions on the food intake of captive rooks (*Corvus frugilegus*). Physiol. Zool. 48: 295-302.

Terrill, S.B. 1987. Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). Behav. Ecol. Sociobiol. 21: 1-11.

Terrill, S.B. & Ohmart, R.D. 1984. Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). Auk 101: 427-438.

Theimer, T.C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 35: 1883-1890.

Thom, V.M. 1986. Birds in Scotland. Poyser, Calton.

Thomas, V.G. 1987. Similar winter energy strategies of grouse, hares and rabbits in northern biomes. Oikos 50: 206-212.

Tinbergen, N. 1939. The behaviour of the snow bunting in spring. Trans. Linn. Soc. N.Y. 5: 1-94.

Townshend, D.J. 1985. Decisions for a lifetime: establishment of spatial defense and movement patterns by juvenile grey plovers (*Pluvialis squatarola*). J. Anim. Ecol. 54: 267-274.

Village, A. 1985. Turnover, age and sex ratios of Kestrels (*Falco tinnunculus*) in South Scotland. J. Zool., Lond. (A). 206: 175-189.

Vincent, J. & Bedard, J. 1976. Fat reserves in snow buntings. Can. J. Zool. 54: 1051-1063.

Vines, G. 1980. Spatial consequences of aggressive behaviour in flocks of Oystercatchers, *Haemotopus ostralegus* L. Anim. Behav. 28: 1175-1183.

Wagner, S.J. & Gauthreaux, S.A.,Jr. 1990. Correlates of dominance in intraspecific and interspecific interactions of song sparrows and white-throated sparrows. Anim. Behav. 39: 522-527.

Waite, T.A. 1987. Vigilance in the White-breasted Nuthatch: effects of dominance and sociality. Auk 104: 429-434.

Waite, T.A. 1992. Winter fattening in Gray Jays: seasonal, diurnal and climatic correlates. Ornis Scand. 23: 499-503.

Watson, A. 1966. Hill birds of the Cairngorms. Scot. Birds 4: 179-203.

Watson, A. 1977. Wildlife potential in the Cairngorms region. Scot. Birds 9: 245-262.

Watson, A. & Smith, R.D. 1991. Scottish Snow Bunting numbers in summer 1970-87. Scot. Birds 16: 53-56.

Watson, J.R. 1970. Dominance-subordination in caged groups of House Sparrows. Wilson Bull. 82: 268-278.

Weatherhead, P.J. & Teather, K.L. 1987. The paradox of age-related dominance in brown-headed cowbirds (*Malothrus ater*). Can. J. Zool. 65: 2354-2357.

Wechsler, B. 1988. Dominance relationships in jackdaws (*Corvus monedula*). Behaviour 106: 252-264.

Wiedenmann, R.N. & Rabenold, K.N. 1987. The effects of social dominance between two subspecies of dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 35: 856-864.

Wiley, R.H. 1990. Prior residence and coat-tail effects in dominance relationships of male dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 40: 587-596.

Wiley, R.H. 1991. Both high- and low-ranking White-throated Sparrows find novel locations of food. Auk 108: 8-15.

Wilson, J.C. 1994. Variation in initiator strategy in fighting by silvereyes. Anim. Behav. 47: 153-162.

Wilson, J.D. & Weir, A.G. 1989. Hunting behaviour and attack success of a female Sparrowhawk between October 1987 and April 1988. Scot. Birds 15: 126-130.

Williamson, K. 1966. The migrations of the snow bunting. In: The snow bunting. (D. Nethersole-Thompson). pp232-257. Oliver & Boyd, Edinburgh and London.

Witter, M.S. & Cuthill, I.C. 1993. The ecological costs of avian fat storage. Phil. Trans. R. Soc. Lond. B 340: 73-92.

Witter, M.S., Cuthill, I.C. & Bonser, R.H.C. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Anim. Behav. 48: 201-222.

Yasukawa, K. & Bick, E.I. 1983. Dominance hierarchies in Dark-eyed Juncos (*Junco Hyemalis*): a test of a game-theory model. Anim. Behav. 31: 439-448.

Zink G. 1985. Der Zug europaischer Singvogel. Vogelwarte Radolfzell, Moggingen.

Zwarts, L., Ens, B.J., Kersten, M. & Piersma, T. 1990. Moult, mass and flight range of waders ready to take off for long-distance migrations. Ardea 78: 339-364.

APPENDIX: Scientific names of species mentioned in the text

Plants

Heather *Calluna vulgaris*

Beech *Fagus sylvatica*

Mammals

Reindeer *Rangifer tarandus*

Stoat *Mustela erminea*

Weasel *Mustela nivalis*

Birds

Mallard *Anas platyrhynchos*

Hen Harrier *Circus cyaneus*

Sparrowhawk *Accipter nisus*

Kestrel *Falco tinnunculus*

Merlin *Falco columbarius*

Peregrine *Falco peregrinus*

Red Grouse *Lagopus lagopus*

Ptarmigan *Lagopus mutus*

Oystercatcher *Haematopus ostralegus*

Golden Plover *Pluvialis apricaria*

Lapwing *Vanellus vanellus*

Semipalmated Sandpiper *Calidris pusilla*

Snipe *Gallinago gallinago*

Turnstone *Arenaria interpres*

Skylark *Alauda arvensis*

Meadow Pipit *Anthus pratensis*

Dipper *Cinclus cinclus*

Fieldfare *Turdus pilaris*

Song Thrush *Turdus philomelos*

Redwing *Turdus iliacus*

Marsh Tit *Parus palustris*

Willow Tit *Parus montanus*

Crested Tit *Parus cristatus*

Great Tit *Parus major*

Silvereye *Zosterops lateralis*

Pinon Jay *Gymnorhinus cyanocephalus*

Mexican Jay *Aphelocoma ultramarina*

Magpie *Pica pica*

Rook *Corvus frugilegus*

Starling *Sturnus vulgaris*

House Sparrow *Passer domesticus*

Snow Finch *Montifringilla nivalis*

Red-eyed Vireo *Vireo olivaceus*

Chaffinch *Fringilla coelebs*

Brambling *Fringilla montifringilla*

Serin *Serinus serinus*

Greenfinch *Carduelis chloris*

American Goldfinch *Carduelis tristis*

Siskin *Carduelis spinus*

Linnet *Carduelis cannabina*

House Finch *Carpodacus mexicanus*

Hawfinch *Coccothraustes coccothraustes*

Evening Grosbeak *Coccothraustes vespertinus*

Yellow-rumped Warbler *Dendroica coronata*

Fox Sparrow *Passerella iliaca*

Field Sparrow *Spizella pusilla*

Harris' Sparrow *Zonotrichia querula*

Song Sparrow *Zonotrichia melodia*

White-crowned Sparrow *Zonotrichia leucophrys*

White-throated Sparrow *Zonotrichia albicollis*

Dark-eyed Junco *Junco hyemalis*

Yellow-eyed Junco *Junco phaeonotus*

Carolina Junco *Junco carolinensis*

Boat-tailed Grackle *Quiscalus major*

Snow Bunting *Plectrophenax nivalis*